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Insects and Other Invertebrates Associated with Flowering Skunk Cabbage, *Symplocarpus foetidus* (L.) Nutt., at Fanshawe Lake, Ontario.¹

By W. W. JUDD²

Introduction

Most of the species of plants in the arum family, Araceae, have their flowers arranged on a central spadix which is surrounded by an enveloping spathe. These floral mechanisms have been classified by Müller (1883). The simplest type, represented by the water-arum, *Calla palustris*, has the spadix fully exposed and the spathe held back from it. Secondly, there is the type in which the spadix is surrounded by the spathe and is only partly visible through the opening of the spathe, as represented by the skunk cabbage, *Symplocarpus foetidus*. Thirdly, there is the most elaborate arrangement, represented by the cuckoo pint, *Arum maculatum*. In this type the spathe surrounds the spadix and is constricted a short distance above its base to form a chamber surrounding the flowers which are concentrated at the base of the spadix. Thus there is formed a "pitfall mechanism" or "kettle trap" which entraps insects that have entered the spathe and ensures the pollination of the flowers by the insects (McLean and Ivimey-Cook, 1956; Müller, 1883).

Observations on these various types of plants have shown that they are visited by many different kinds of insects and other invertebrates including flies, beetles, bugs, bees, slugs and snails, many of which have been found transporting or eating the pollen (Kerner and Oliver, 1895; Knuth, 1906, 1909; Müller, 1883). The nectar and odour of the plants may play a role in attracting the visitors. Once they have entered the spathe temperature may play a part in keeping them there, for several observations have shown that the temperature in the spathes of plants growing during cold weather may be as much as 29° F above that of the immediate environment (Kerner and Oliver, 1894). Predaceous spiders have also been found frequently in the spathes, either lying in wait for insect prey or spinning webs across the mouth of the spathe (D'Ewes, 1959; Trelease, 1879). Invertebrates in the spathes may in turn be food for small vertebrates such as the Arum Frog, *Hyperolius horstocki*, which lives in the spathe of the African "Pig Lily", *Zantedeschia aethiopica* (D'Ewes, 1959).

In the case of the skunk cabbage, *Symplocarpus foetidus*, studies have been made which demonstrate that this plant is visited during flowering by honey bees, bugs, small flies, beetles, slugs and spiders (Trelease, 1879) and that later in the season, when the spathes are rotting, the plants are occupied by small flies, particularly of the families Psychodidae, Drosophilidae and Chloropidae (Brown, 1956). During March, April and May of 1959 an opportunity was taken of following the course of development of plants of skunk cabbage on the north shore of Fanshawe Lake near London, Ontario and of determining the succession of appearance of various kinds of insects and other invertebrates on the plants. The present paper is a report on this project.

Methods

The place at which the skunk cabbages were studied was on the north shore of Fanshawe Lake which is formed by the damming of the North Branch of the

¹Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the government of Ontario granted through the Ontario Research Foundation.

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Thames River and which is under the jurisdiction of the Upper Thames River Conservation Authority. The map (Fig. 1) was traced from aerial photographs kindly supplied by the Authority. The north end of the lake is about five miles northeast of London, Ontario and lies partly in the Township of London and partly in the Township of West Nissouri. At this point the lake is about 400 feet wide at low water level and is bordered by a flood plain, the water level being about 825 feet above sea level. On the south of the lake the flood plain gives way to low ground occupied by willow scrub and on the north to an abrupt clay cliff rising to a crest 900 feet above sea level. The crest and slopes of the cliff are occupied by deciduous woods, and cultivated fields extend northward from these woods. The McIlwraith Ornithological Club of London has a nature trail which extends in a narrow loop for somewhat less than a half-mile westward from the boundary between London and West Nissouri Townships. The upper part of the trail skirts the woods on the top of the cliff and the lower part winds along a narrow path through the woods about half way down the cliff. The patch of skunk cabbage under study was directly below the nature trail in heavy black muck. The area marked for study was rectangular, of dimensions 105 ft. x 15 ft. (Fig. 1-A). This area was horizontal and was unshaded from the south so all parts of it received equally the full impact of the sun's rays through the day. During the period of study the soil was constantly saturated owing to seepage and run-off of water from the slopes above.

During March, April and May observations were made daily on the plants in the cabbage patch. As each spathe opened to disclose the spadix the plant was marked with a numbered stick stuck into the soil beside it. The number of spathes opening each day was recorded. Each day all the open spathes in the patch were examined for the presence in them of insects and other invertebrates. These creatures were removed from the spathes with forceps or were sucked up into an aspirator inserted into the spathe and were placed in poison jars. The specimens were pinned or preserved in fluid and each was labelled to show the number of the spathe from which it was taken and the date of its collection. The specimens were examined under the microscope for the presence of skunk cabbage on them. The pollen was recognizable from keys and descriptions in Erdtman (1952), each grain being a broad oval of dimensions $35 \mu \times 27 \mu \times 23 \mu$ with a reticulated surface and a sulculus encircling its equator. As the season progressed the leaves unrolled and opened out flat and the number of leaves opening out flat each day was recorded. As each flattened leaf was counted a triangular nick was cut out of its edge in order that it would not be counted again. The leaves in the patch were scanned each day and insects and other invertebrates on them were collected. Observations on the plants were discontinued on May 20. Readings of temperature and snow cover were taken from the Monthly Meteorological Summary of the Meteorological Division of the Department of Transport, based upon observations taken at Crumlin Airport which lies about three miles south of the location of the skunk cabbage patch.

Most of the specimens collected were identified by the following taxonomists, who, unless otherwise noted, are staff members of the Entomology Research Division, United States Department of Agriculture: C. P. Alexander, University of Massachusetts (Trichoceridae), G. E. Ball, University of Alberta (Carabidae), N. B. Causey, Fayetteville, Arkansas (Diplopoda), J. G. Chilcott, Canada Department of Agriculture (Muscidae), C. D. Dondale, Canada Department of Agriculture, Kentville, N.S. (Arachnida), E. J. F. Marx, Merchantville, N.J., and J. A. Wilcox, New York State Museum, Albany (*Donacia*), C. W. Sabrosky (Sepsidae, Sphaeroceridae), H. van der Schalie, University of Michigan (Suc-

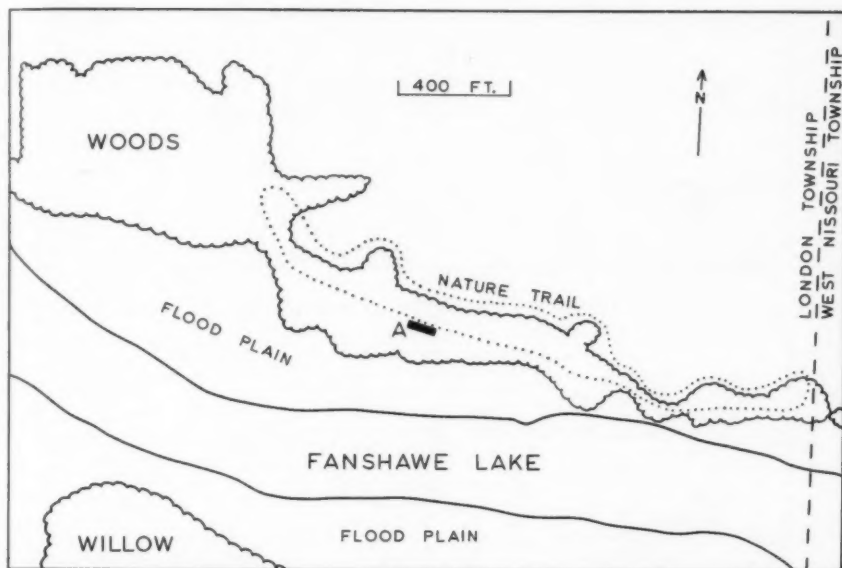


Fig. 1. Map showing location of skunk cabbage patch (A) at north end of Fanshawe Lake.

cineidae), G. B. Vogt (Chrysomelidae), W. W. Wirth (Phoridae, Syrphidae). The remaining specimens were identified by the writer using keys in Blatchley, 1926 (Hemiptera), Kelton, 1955 (*Liocoris*), Pilsbry, 1948 (*Deroceras*), Viereck, 1916 (*Apis*) and Walker, 1927 (Isopoda). All specimens are deposited in the collections of the Department of Zoology, University of Western Ontario except those noted in the following account as being "retained" in the collections of the institutions in which they were identified.

Succession of Events in the Growth of *Symplocarpus*

The first spathe opened on March 5 when its anthers were found covered with pollen; on March 6 three more spathes opened and the flowers likewise were well covered with pollen, some of which collected as yellow dust in the bottom of the spathe (Fig. 2-b). These spathes opened during a time when the daily maximum temperature had been above freezing for several days (Fig. 2-d). The remaining spathes opened in three periods (Fig. 2-b) which occurred during times when the maximum temperatures were above freezing, March 14-15, March 18-20 and March 23-April 8. The times between these periods were characterized by maximum temperatures being at or below freezing (Fig. 2-d). Most of the spathes opened during the period March 23-April 8. The greatest number of spathes, 73, opened on March 26 (Fig. 2-b, Fig. 3-a). Altogether the plants in the study area produced 714 spathes which opened between March 5 and April 8 (Fig. 2-a). Most of the spathes opened while snow still lay on the ground. The last trace of snow disappeared on April 5 (Fig. 2-c). During the remainder of the season the spathes slowly rotted away and by May 14 they had all rotted, leaving the spadices standing erect in the mud (Fig. 3-a).

While the spathes were developing the leaves were appearing as narrow, conical spikes which gradually unrolled as they lengthened. By April 19 the leaves on most of the plants had grown above the tops of the spathes. The first

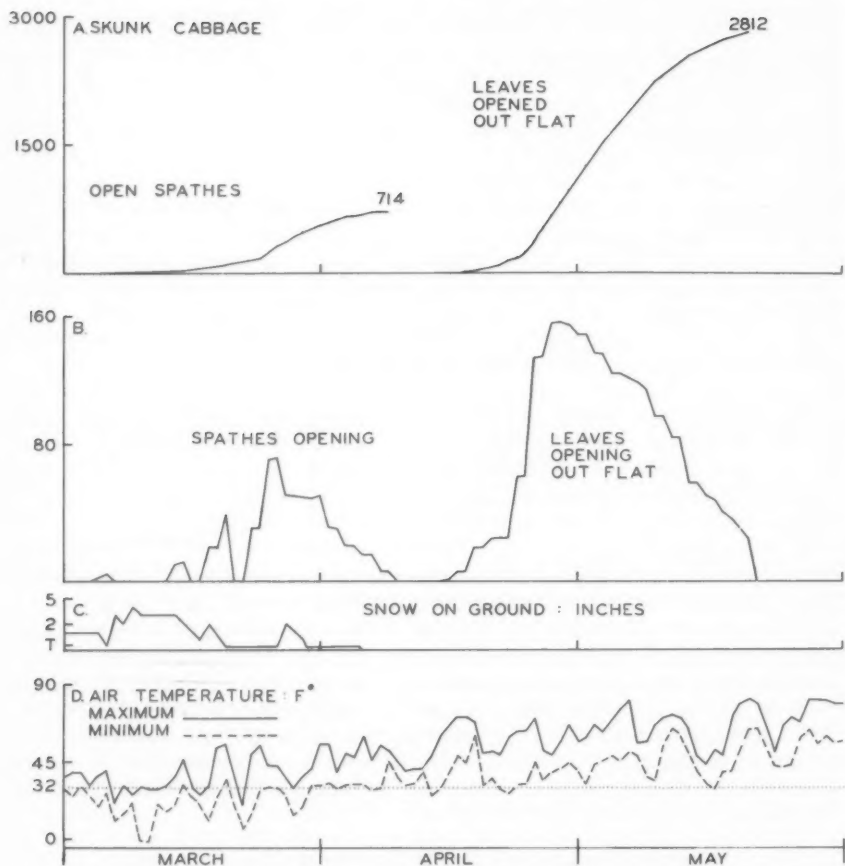


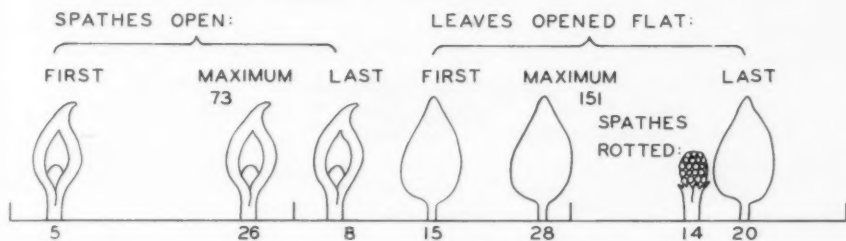
Fig. 2. A, Number of open spathes and leaves; B, Periods of opening of spathes and leaves; C, Snow cover on ground (T = trace, i.e. less than 1 inch); D, Air temperatures.

leaf opened out flat on April 15 (Fig. 2-a, b, Fig. 3-a). Thereafter the leaves opened out flat rapidly with the greatest number, 151, opening on April 28 (Fig. 2-b, 3-a). Altogether the plants in the study area produced 2,812 leaves which opened out between April 15 and May 20 (Fig. 2-a).

Account of Invertebrates on Plants

The first spathe opened on March 5 and on the following day, March 6, three more spathes opened. In two of these a female crane-fly, *Trichocera* (*garretti*?), liberally dusted with pollen, was found perched on the spadix and in the third a hump-backed fly, *Triphleba fusca*, was found between the spathe and the base of the spadix (Fig. 3-b). During the second period of opening of spathes, March 14-15, spiders first appeared in the spathes (Fig. 3-b), the two species occurring at this time being *Enoplognatha marmorata*, dusted with pollen, on March 14 and *Schizocosa crassipes* on March 15. During the third period of opening of spathes, March 18-20, two harvestmen, *Leiobunum dorsatum*, dusted with pollen, first appeared together in one spathe on March 20 (Fig. 3-b). As

A. GROWTH OF SKUNK CABBAGE



B VISITORS AT PLANTS : DATE OF FIRST APPEARANCE

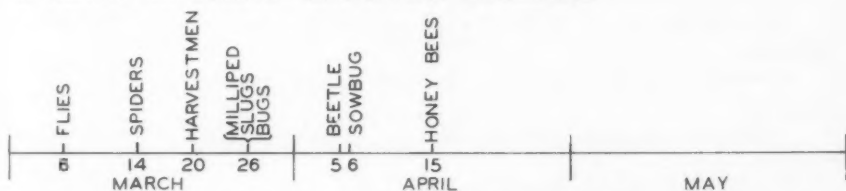


Fig. 3. A, Succession of events in growth of skunk cabbage; B, Dates of first appearance of invertebrates in spathes.

the final period of opening of spathes started on March 26 millipeds, slugs and plant bugs appeared in the spathes and thereafter a beetle, sowbugs and honey bees appeared in succession (Fig. 3-b). The following account shows what invertebrates visited the spathes and leaves, together with the times of their appearance. Species marked (#) were represented by some specimens found dusted with pollen.

Invertebrates in Spathes**Gastropoda****Limacidae**

Deroceras reticulatum (Müller) — 11 slugs, March 26-April 19.

Isopoda**Trichoniscidae**

Trichoniscus sp. — 1 sowbug, April 6; 2 in decaying spathe, May 14.

Oniscidae

Porcellio rathkei Brandt — 3 sowbugs in decaying spathe, May 14.

Diplopoda**Julidae**

Ophiulus fallax (Meinert) — 3 millipeds, March 26, 28, April 19; several in decaying spathes, May 14.

Cylindroiulus teutonicus (Pocock) — several millipeds in decaying spathes, May 14.

Arachnida**Phalangiidae**

Leiobunum dorsatum (Say) — 6 harvestmen, March 20-29 (1 retained).

Amaurobiidae

Amaurobius ferox (Walkenaer) — 1 spider, March 24.

Theridiidae

Enoplognatha marmorata (Hentz) — 13 spiders, March 14-April 17 (2 retained).

Linyphiidae

Lepthyphantes zebra (Emerton) — 1 spider, March 24 (retained).

Linyphia waldea C. and I. — 1 spider, March 30 (retained).

Linyphiid — 1 spider, March 26 (retained).

Erigonidae

Erigonid — 1 spider, March 26 (retained).

Argiopidae

Tetragnatha sp. — 1 spider, March 29.

Pachygnatha kuratai Levi — 2 spiders, April 5, 7 (retained).

Pachygnatha sp. — 1 spider, April 2 (retained).

Hahniidae

Neoantistea radula (Emerton) — 1 spider, April 3 (retained).

Lycosidae

Schizocosa crassipes (Walckenaer) — 5 spiders, March 15-April 3 (1 retained).

Pirata sp. — 6 spiders, March 26-April 2.

Pardosa xerampelina (Keyserling) — 1 spider, April 3.

Thomisidae

Xysticus triguttatus Keyserling — 2 spiders, March 25, 29 (1 retained).

Attidae

Synemosina formica Hentz — 1 spider, March 24 (retained).

Phidippus audax Hentz — 1 spider, April 22 (retained).

Hemiptera

Miridae

Liocoris rufidorsus Kelton — 6 plant bugs, March 26-April 17; one of these bugs was caught in a spider web in a spathe on March 30.

Reduviidae

Zelus exsanguis (Stal) — 1 nymph, March 30.

Coleoptera

Carabidae

Pterostichus luctuosus Dejean — 1 beetle, April 5.

Hymenoptera

Apidae

Apis mellifera L. — 3 honey bees, April 15

Diptera

Trichoceridae

Trichocera (garretti) Alex. ? — 2 female craneflies, March 6.

Phoridae

Triphleba subfusca Müller — 1 fly, March 6 (retained).

Sphaeroceridae

Leptocera sp. — 4 flies, March 31; 1 fly, April 2.

Sepsidae

Sepsis punctum (F.) — 1 fly, April 15.

Sepsis neocynipsea M. and S. — 1 fly, April 16.

Syrphidae

Tubifera dimidiata (Wied.) — 1 fly, April 16.

Muscidae

Eremomyioides cylindrica (Stein) — 1 fly, April 4; 4 flies, April 8 (retained).

Invertebrates on Leaves**Gastropoda**

Succineidae

Oxyloma decampi gouldi Pilsbry — 2 snails, April 16 (retained).

Arachnida

Clubionidae

Clubiona mixta Emerton — 1 spider in web in a rolled leaf, April 17 (retained).

Hemiptera

Pentatomidae

Euschistus tristigmus (Say) — 2 stink bugs, May 3, 20.

Euschistus variolarius (P. de B.) — 1 stink bug, May 2.

Cosmopepla bimaculata (Thomas) — 1 stink bug, May 20.

Cydnidae

Sebirus cinctus (P. de B.) — 1 burrowing bug, May 20.

Coleoptera

Chrysomelidae

Coreopsomela sp. — 3 beetles, May 2; 3 beetles, May 3.

Zygospila sp. — 1 beetle, May 20.

Donacia sulcicollis LaCordaire — 8 beetles, May 20.

Donacia flavipes Kirby — 4 beetles, May 20.

Discussion of Collections

It is evident from the foregoing observations that as soon as the spathes of skunk cabbage first opened there were insects present which entered them and became covered with pollen and thus were capable of transferring pollen from one plant to another. Collections of insects and other invertebrates were made from 82 (12%) of the 714 spathes in the study area. This number includes several spathes from which more than one collection of visiting creatures was made during March and April. Doubtless other visitors entered the spathes when collections were not being made.

Eleven slugs, *Deroceras reticulatum*, were found in or on the spathes, some of them moving over the surface of the spadix. None were found with pollen on them. Several authors include various species of slugs as visitors at plants of the arum family (Knuth, 1906; Trelease, 1879). One sowbug, *Trichoniscus* sp., was found in a flowering spathe, but most of the sowbugs were found later in the season on decaying spathes. Three millipeds were found in flowering spathes, one being liberally dusted with pollen, but most of them, like the sowbugs, were found in the bases of rotting spathes in May. Both species collected, *Ophiulus fallax* and *Cylindroiulus teutonicus*, have been introduced from Europe (Chamberlin and Hoffman, 1958). Six harvestmen, *Leiobunum dorsatum*, were found in spathes, some of them dusted with pollen. Gertsch (1948) reports that in the north most harvestmen die in the autumn but that a single species, *Leiobunum formosum*, is known to live over winter as an adult. It is likely that the six specimens of *L. dorsatum* found in the spathes had survived the winter for they were all collected in March.

The creatures found most commonly in the spathes were spiders, representing nine families and at least eleven species. They were found either on webs spun between the spathe and the spadix or crouched in the spathe at the base of the spadix. Only one captive insect, a bug, *Liocoris rufidorsus*, was found in a web in a spathe. Descriptions by Gertsch (1948) of the various families and species included in the collections show that spiders of all sorts of habits and habitats were represented: some make webs and some do not, some live under shelters and some in the open, some lie in wait for prey and others search for it, some are "walking" spiders and some are "jumping" spiders. The spider most commonly found, *Enoplognatha marmorata*, appeared to be best adapted to secreting itself in the spathe. It was usually found among the flowers at the base of the spadix. In size and shape it resembled closely a male flower in full pollen production. Thus, when crouched among the flowers and liberally dusted with pollen, it was often overlooked at first unless it moved. Trelease (1879) in his study of skunk cabbage reports finding spiders "whose webs bar the entrance to three-fourths of the spathes" and D'Ewes (1959) records finding two species of spiders in the spathe of the African Pig Lily.

The plant bugs, *Liocoris rufidorsus*, were found moving actively over the spadices of the plants and were dusted with pollen. This species overwinters in the adult stage (Kelton, 1955). The nymph of the assassin-bug, *Zelus exsanguis*, was also covered with pollen which clung to the bug's sticky exterior. This insect also overwinters (Blatchley, 1926). The only beetle found in the spathes, *Pterostichus luctuosus*, was in the base of the spathe and is a ground beetle which occurs beneath rubbish, usually near water, and hibernates in the adult stage (Blatchley, 1910). Honey bees, *Apis mellifera*, were first found visiting the plants on April 15. Their pollen baskets were loaded with skunk cabbage pollen and they were the only insects actually seen flying from plant to plant. They collected pollen actively on sunny days in April as long as the plants were producing pollen and later during April and May they visited plants of hepatica, bloodroot and dog's-tooth violet as these plants came into bloom on the face of the cliff.

The first collections of insects from the spathes, on March 6, included two female *Trichocera* (*garretti*?). Identification of the species was not possible for examination of the male genitalia is necessary to identify the species. Flies of the genus *Trichocera* are the "winter crane-flies" which occur in spring and may appear on warm days in winter (Alexander, 1942). *T. garretti* has been reported in Ontario at Hamilton by Judd (1949) who found one in flight on March 14, 1948 at the Dundas Marsh when the water was still frozen and covered with snow and the flowers of skunk cabbage were producing pollen. Flies in five other families were found in the spathes. Adults of Phoridae, Sphaeroceridae and Sepsidae are found particularly about decomposing vegetation in swampy places (Curran, 1934), and adults of many species of Syrphidae and Muscidae are recorded as visitors at flowers (Knuth, 1909).

The invertebrates found on the leaves included two snails, *Oxyloma decampi gouldi* (a species recorded from Ontario by LaRocque, 1953) which were not feeding but were withdrawn into their shells and a single spider, *Clubiona mixta*, crouched in its web at the base of a rolled leaf. The insects found on the leaves were evidently using them only as temporary resting places for none were found feeding. The three stink bugs and the burrowing bug, *Sebirus cinctus*, overwinter as adults and on emerging in spring fly to foliage and flowers (Blatchley, 1926). The leaf beetles *Coreopsomela* and *Zygospila*, include species which feed on plants other than skunk cabbage (Achard, 1923; Brown, 1945; Monrós,

1955). Hoffman (1939), Marx (1957) and Schaeffer (1925) report that larvae of *Donacia* live on the roots and lower leaves of various aquatic plants and Blatchley (1910) reports some species of *Donacia* adults found on the leaves and the roots of skunk cabbage.

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(Received June 9, 1960)

**Resistance of Spring Wheats to the Wheat Stem Sawfly,
Cephus cinctus Nort. (Hymenoptera: Cephidae)
I. Resistance to the Egg¹**

By N. D. HOLMES AND L. K. PETERSON

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Under certain environmental conditions the resistance of wheats to the wheat stem sawfly, *Cephus cinctus* Nort., may be reduced or even lost. In addition, these varieties are not suitable for all of the region where the sawfly is a problem. To assist in the improvement of the presently resistant wheats, studies were begun in 1953 to determine the nature of the resistance to the sawfly. The present paper deals with the effects of various spring wheats and of different parts of the stems of these wheats on the hatching of the egg of the sawfly and presents evidence for hypotheses on the cause of these effects. Although several authors have reported on resistance to the sawfly (Ainslie, 1920; Criddle, 1915, 1922; Farstad, 1940; Farstad and Platt, 1946; Kemp, 1934; Platt *et al.*, 1948; Roemhild, 1954; Roberts, 1954), none has dealt with the effects of the host on the egg alone.

Materials and Methods

The varieties tested included the bread wheats (*Triticum aestivum* L. emend Thell.) Red Bobs, Rescue and S-615; and the durum wheats (*T. durum* Desf.) Golden Ball and Stewart. One variety of oats, Victory, was also examined. Rescue, S-615 and Golden Ball are solid-stemmed and resistant to the sawfly. Stewart is mostly hollow-stemmed and has some resistance, whereas Red Bobs is hollow-stemmed and susceptible to sawfly damage. Oats are hollow-stemmed but are immune.

The experiments were done between 1953 and 1959 at Lethbridge. The test varieties, which were seeded on dry land next to wheat stubble containing large numbers of *C. cinctus*, received infestations under natural conditions. All varieties were not tested in every year. The oats were grown only in 1955, S-615 only in 1959 and Stewart in 1954, 1955 and 1956. Golden Ball was not tested in 1953 and both Golden Ball and Red Bobs were omitted in the 1959 test. Where insufficient data were obtained they were either omitted or indicated by a dash in the tables.

The varieties were seeded in randomized plots with four replications. At least 50 infested stems of each variety were examined on each date of observation. The infestations and mortalities were obtained by splitting the stems longitudinally and examining them under a stereoscopic microscope. As the internodes elongate successively starting with the basal internode, they were numbered in the order in which they elongated.

Eggs deposited in a hollow-stemmed host lie on the inner wall of the stem (Fig. 1). They are usually dispersed within the stem so that, unless infestations are heavy, most escape attack by the larvae that hatch first. With the exception of the second and third dates of seeding in 1954, examinations were started as soon as the flight ended and were continued at intervals of two or three days. Eggs that were damaged by larvae could be easily recognized. These were not used in the calculations of egg mortality. In the solid-stemmed hosts the eggs lie in small excavations in the pith, and as the eggs are generally separated by the pith, the numbers that escape larval attack are greater than in the hollow-stemmed varieties. The pith tissues around the excavations often become brown in four

¹Contribution from the Entomology Section.

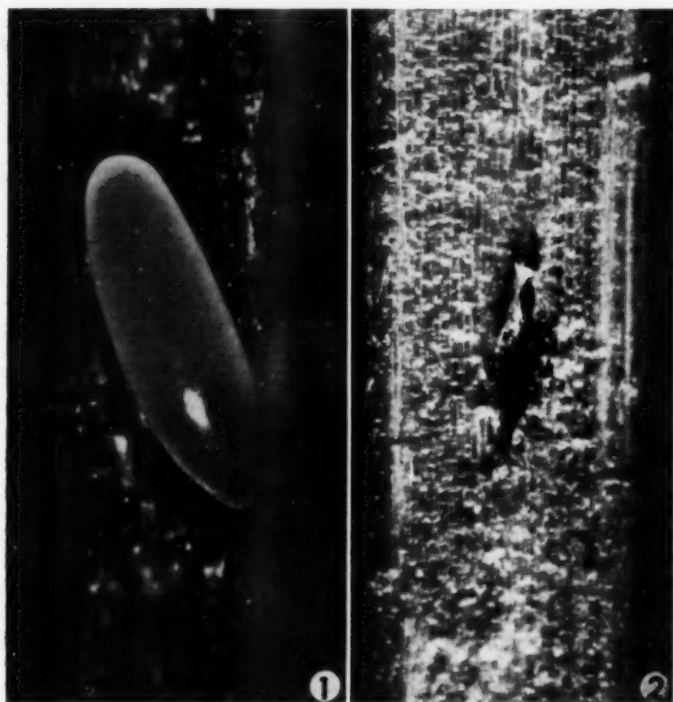


Fig. 1. Sawfly egg in cavity of stem.

Fig. 2. Dead sawfly egg in pith of Rescue wheat.

or five days after oviposition and hence assist the observer in finding the eggs. Eggs that die collapse (Fig. 2).

In addition to the field tests, eggs removed from stems were tested in the laboratory for hatching in distilled water, solutions of sodium chloride and expressed wheat stem juice.

Effects of Various Factors on Survival of Eggs in the Field Environment

Survival varied not only between host varieties but also within varieties when seeded on different dates and in different years (Table I).

Survival of the eggs also usually varied between internodes of the same stems. In Golden Ball the percentages of eggs in each internode that died were:

| Year | Date seeded | Internode | | | |
|-------|-------------|-----------|----|----|----|
| | | 1 | 2 | 3 | 4 |
| 1954 | May 7 | — | 5 | 8 | 15 |
| | May 18 | — | 72 | 78 | 56 |
| | June 3 | 64 | 70 | 44 | — |
| 1955 | May 6 | 85 | 69 | 58 | 31 |
| | May 26 | 41 | 55 | 53 | — |
| 1956 | May 8 | — | 45 | 37 | 44 |
| 1957 | May 1 | 47 | 33 | 26 | — |
| 1958* | April 24 | 45 | 37 | 52 | — |
| 1958* | April 24 | 30 | 30 | 30 | 28 |

*Concurrent tests.

TABLE I

Percentages of eggs dead at hatching time in several wheats sown on different dates and in different years.

| Year | Date seeded | Variety | | | |
|------|-------------|----------|--------|-------------|---------|
| | | Red Bobs | Rescue | Golden Ball | Stewart |
| 1953 | May 6 | — | 3 | — | — |
| 1954 | May 7 | 7 | 11 | 9 | 3 |
| 1955 | May 6 | 12 | 55 | 66 | 40 |
| | May 26 | 2 | 27 | 49 | 34 |
| | June 6 | 2 | 19 | — | — |
| 1956 | May 8 | 0 | 22 | 46 | 17 |
| 1957 | May 1 | 3 | 32 | 48 | — |
| 1958 | Apr. 24 | 11 | 9 | 28 | — |
| 1959 | May 8 | — | 29 | — | — |

Mortality was not consistently greater in any one internode. Maturity of the stem appeared to have little effect on the mortality. The eggs are laid in Internode 1 when the stems are very young and in progressively higher internodes as the stems mature (Holmes and Peterson, 1960). Hence, whatever the date or year a variety was seeded the stems were at about the same physiological age when corresponding internodes were infested. Resistance of each internode varied between dates of seeding, showing that resistance of the internodes was mostly influenced by the environment during the growing season. Similarly, as each internode of the same stem develops in a different environment, differences in resistance among different internodes of the same stems also appear to be mostly determined by the environment.

In Rescue the survival of eggs laid in the pith was compared with that of eggs laid in the cavities of the same stems. The distribution of oviposition sites was not changed by the presence of pith; examinations of Red Bobs and Rescue stems in 1953 showed that the sawflies oviposited at the same sites in the internode whether it was solid or not. The angular transformations of egg mortality in cavities and in pith in Rescue in 1954 were:—

| Oviposition site | Date seeded | | |
|------------------|-------------|--------|--------|
| | May 7 | May 18 | June 3 |
| Cavity | 2.41 | 22.25 | 22.70 |
| Pith | 35.61 | 39.01 | 37.47 |

L.S.D. at the five per cent level between positions: 14.34

Mortality in the cavities was about equal to that expected in susceptible hollow-stemmed hosts, whereas mortality in the pith was significantly higher than that in the cavity for each date of seeding.

The mortality in Rescue pith varied from only six per cent in 1953 to 60 per cent in 1955. As in Golden Ball, mortality in the pith in Rescue varied between internodes of the same stems and between corresponding internodes in plants seeded on different dates and years (Table II). As for Golden Ball, the mortality in the pith evidently depends largely on the environment in which the internode develops. Nevertheless, the pith is obviously the major factor in egg mortality.

TABLE II

Percentage of eggs that died in the pith and in the cavity of each internode of Rescue seeded on different dates.

| Year | Date seeded | Internode | | | | | | | |
|------|-------------|-----------|------|--------|------|--------|------|--------|------|
| | | 1 | | 2 | | 3 | | 4 | |
| | | Cavity | Pith | Cavity | Pith | Cavity | Pith | Cavity | Pith |
| 1954 | May 7 | — | — | — | — | 0 | 11 | 10 | 23 |
| 1955 | May 6 | 0 | 75 | 0 | 86 | 15 | 50 | 0 | 17 |
| | May 26 | 0 | 62 | 11 | 21 | 0 | 43 | — | — |
| | June 6 | 0 | 22 | 0 | 30 | 0 | 50 | — | — |
| 1956 | May 8 | — | — | — | 33 | 0 | 33 | 0 | 40 |
| 1957 | May 1 | — | 19 | 0 | 38 | 0 | 24 | 14 | 14 |
| 1959 | May 8 | — | 50 | — | 53 | — | 45 | — | 29 |

In Red Bobs seeded on May 6, 1955, the bottom internode was solid and 27 per cent of the eggs in it died. The second internode was less solid and egg mortality in it was 13 per cent. The remaining internodes were hollow and the mortalities in them ranged from zero to four per cent. In Red Bobs seeded on May 26 and June 6 in 1955 the stems were completely hollow, as is normally expected, and the egg mortalities did not exceed three per cent in any internode. In 1955 in Victory oats, which was 89 per cent infested, mortality was as low as in Red Bobs.

Stewart is normally hollow-stemmed with thick walls and is usually fairly susceptible to sawflies. However, under certain environmental conditions the lower internodes become solid, as in 1955. The percentages of eggs that died in the pith and in the cavity of the various internodes of Stewart in 1955 and 1956 were:—

| Year | Date seeded | Internode | | | | | | | |
|------|-------------|-----------|------|--------|------|--------|------|--------|------|
| | | 1 | | 2 | | 3 | | 4 | |
| | | Cavity | Pith | Cavity | Pith | Cavity | Pith | Cavity | Pith |
| 1955 | May 6 | 29 | 92 | 28 | 75 | 0 | — | 0 | — |
| 1956 | May 26 | 24 | 86 | 17 | 60 | 0 | — | — | — |
| | May 8 | 18 | — | 11 | 100 | 17 | — | 0 | — |

Here again most mortality occurred in the pith although the mortalities in the cavities of Internodes 1 and 2 were higher than those in the cavities of Rescue and Red Bobs seeded on the same dates.

The mortality in the pith varied not only between the various internodes but also within the same internode (Table III). In the pith of about 40 per cent of the Golden Ball internodes and of 20 to 50 per cent of those of Rescue some eggs died and others hatched. The percentages of internodes in which all of the eggs hatched in the pith averaged higher in Rescue than in Golden Ball.

TABLE III

Percentages of internodes of Rescue and Golden Ball in which various percentages of the eggs in the pith died

| Variety of wheat | Year | Date seeded | Percentage mortality* | | |
|------------------|------|-------------|-----------------------|------|----|
| | | | 100 | 1-99 | 0 |
| Rescue | 1955 | May 6 | 62 | 27 | 12 |
| | | May 26 | 26 | 19 | 55 |
| | | June 6 | 21 | 29 | 50 |
| | 1957 | May 1 | 13 | 43 | 45 |
| | 1959 | May 8 | 17 | 51 | 31 |
| Golden Ball | 1955 | May 6 | 45 | 48 | 8 |
| | | May 26 | 40 | 40 | 20 |
| | 1956 | May 8 | 23 | 37 | 41 |
| | 1957 | May 1 | 33 | 37 | 29 |
| | 1958 | Apr. 24 | 11 | 47 | 42 |

*Based only on internodes with at least two eggs in the pith.

Numbers of Eggs Per Stem or Internode

In 1955, the number of eggs laid in each stem was related to the number laid in the pith of the resistant varieties. The cavities in solid-stemmed varieties are usually limited to the top of each internode, and as the number of eggs per stem increased the number laid in the lower part of each internode also increased. The correlation coefficients between the number of eggs in the pith and the number per stem were:—

| Date seeded | Host variety | | |
|-------------|--------------|-------------|---------|
| | Rescue | Golden Ball | Stewart |
| May 6 | 0.632** | 0.720** | 0.891** |
| May 26 | 0.617 | 0.912** | 0.975** |

**Significant at one per cent level.

Therefore, an increase in the number of eggs laid in a solid-stemmed variety does not necessarily result in an equivalent increase in the number of larvae.

The 1955 data also suggested that an increase in oviposition resulted in poorer survival of the eggs in both cavity and pith. Correlation coefficients between the numbers of eggs per stem and the percentages that hatched in the cavity and in the pith were:—

| Host variety | Date seeded | Location of eggs | |
|--------------|-------------|------------------|----------|
| | | Cavity | Pith |
| Rescue | May 6 | -0.518 | -0.435 |
| | May 26 | -0.976 | -0.656 |
| Golden Ball | May 6 | — | -0.697** |
| | May 26 | — | -0.989** |
| Stewart | May 6 | -0.960** | -0.808 |
| | May 26 | -0.954** | -0.979 |

**Significant at one per cent level.

TABLE IV

Percentage mortalities of eggs in the pith of internodes of three wheats according to the number of eggs per internode, 1955-1959

| Variety of wheat | Year | Number of eggs per internode | | | |
|------------------|--------|------------------------------|----|----|-----|
| | | 1 | 2 | 3 | 4 |
| Rescue | 1955* | 48 | 58 | 89 | — |
| | 1955** | 31 | 31 | 42 | — |
| | 1957 | 32 | 31 | 37 | 40 |
| | 1958 | 31 | 40 | 24 | 35 |
| | 1959 | 23 | 39 | 48 | 45 |
| Golden Ball | 1955* | 60 | 70 | 71 | 69 |
| | 1955** | 39 | 56 | 58 | 54 |
| | 1956 | 23 | 38 | — | — |
| | 1957 | 38 | 40 | 93 | 63 |
| | 1958 | 19 | 31 | 42 | 38 |
| Stewart | 1955* | 78 | 96 | 96 | 100 |
| | 1955** | 77 | 90 | 86 | — |

*Seeded on May 6.

**Seeded on May 26.

All three varieties showed a negative relationship. In the cavities, the hatch in Rescue fell only to 83 per cent and in Stewart to 76 per cent while the numbers of eggs per stem increased from one to six. However, in the pith of Rescue and Golden Ball, the percentage that hatched decreased from about 70 to about 20.

Examination of the mortalities in internodes of solid-stemmed varieties for several years also suggested that the number of eggs laid in the pith of an internode influenced the percentage that died in that internode (Table IV). In all three varieties, Rescue, Golden Ball and Stewart, when only one egg was laid in the pith of an internode it had a better chance of hatching than had those in internodes where two or more eggs had been laid. Chi-square values, significant at the five per cent level, of 9.77 and 11.62 for Rescue and Golden Ball were obtained for mortalities of only one egg per internode.

These results raise two questions. Were the internodes that received only one or two eggs originally less resistant than those that received the higher numbers of eggs? The differences in egg survival could then be attributed to the internode infested and not to the number of eggs that were deposited in the internode. Conversely, were the differences in resistance observed between internodes actually only the result of differences in the numbers of eggs laid per internode? The data show that the differences in egg survival between internodes are the result of differences in the resistance of the pith of those internodes, and that increased frequency of oviposition per internode does increase egg mortality. In 1955, the percentage mortalities of the single eggs in the pith calculated for each internode, compared with the percentage mortalities of all eggs in the pith of each internode, in parentheses, were:

| Variety | Date seeded | Internode | | | |
|-------------|-------------|-----------|---------|---------|---------|
| | | 1 | 2 | 3 | 4 |
| Rescue | May 6 | 56 (75) | 62 (86) | 17 (50) | — |
| | May 26 | 45 (62) | 17 (21) | 36 (43) | — |
| Golden Ball | May 6 | 56 (85) | 50 (69) | 44 (58) | 37 (31) |
| | May 26 | 19 (41) | 37 (55) | 37 (53) | — |

TABLE V

Percentage mortalities of eggs in the pith of corresponding internodes of two wheats according to the number of eggs in the pith per internode in 1959

| Variety | No. of eggs per internode | Internode | | | | | Average |
|---------|---------------------------|-----------|----|----|----|----|---------|
| | | 1 | 2 | 3 | 4 | 5 | |
| Rescue | 1 | 25 | 35 | 6 | 14 | 6 | 17 |
| | 2 | 46 | 45 | 21 | 32 | — | 37 |
| | 3 | 33 | 44 | 43 | 11 | — | 36 |
| | 4+ | 50 | 41 | 36 | 22 | — | 37 |
| | Average | 39 | 41 | 27 | 20 | — | |
| S-615 | 1 | 44 | 18 | 25 | 34 | 33 | 31 |
| | 2 | 72 | 29 | 41 | 70 | 50 | 52 |
| | 3 | 78 | 35 | 49 | 83 | — | 61 |
| | 4+ | 60 | 47 | 61 | 68 | — | 59 |
| | Average | 64 | 32 | 44 | 64 | 41 | |

The percentage mortalities of single eggs not only were substantially lower than those for all eggs in corresponding internodes, but their values were largely in proportion to those for all eggs.

The 1959 data for Rescue provided further support (Table V). The results were similar in S-615; in almost every internode mortality was lowest for single eggs.

Host Maturity

Because the sawfly usually selects the upper two internodes that are elongating at the time, the eggs are laid in progressively higher internodes as the stem matures (Holmes and Peterson, 1960). Hence, one can determine the effect of host maturity at oviposition time on egg mortality by comparing the mortalities in different internodes of the same stems.

Internodes of Rescue vary in solidness within the same stem. Generally, the lowest two have short cavities and the rest progressively longer ones. The relative lengths of the cavities are affected by environmental conditions, but almost invariably the top two internodes have the longest cavities (Holmes *et al.*, 1960).

The data from Rescue seeded on three dates in 1955 show the complexity of this relationship and the necessity of careful analysis of each factor. The percentages of eggs that died in the stems of plants seeded on May 6 and 26 and June 6 were 55, 27 and 19. It would appear superficially that the resistance to egg development increased as the plants matured. However, although age of the stem did have an effect, it was only by way of its influence on where the eggs were laid. The percentages of eggs laid in each internode of these stems were:

| Date seeded | Internode | | | | |
|-------------|-----------|----|----|----|---|
| | 1 | 2 | 3 | 4 | 5 |
| May 6 | 13 | 28 | 45 | 15 | 1 |
| May 26 | 16 | 41 | 36 | 8 | 0 |
| June 6 | 31 | 63 | 6 | 0 | 0 |

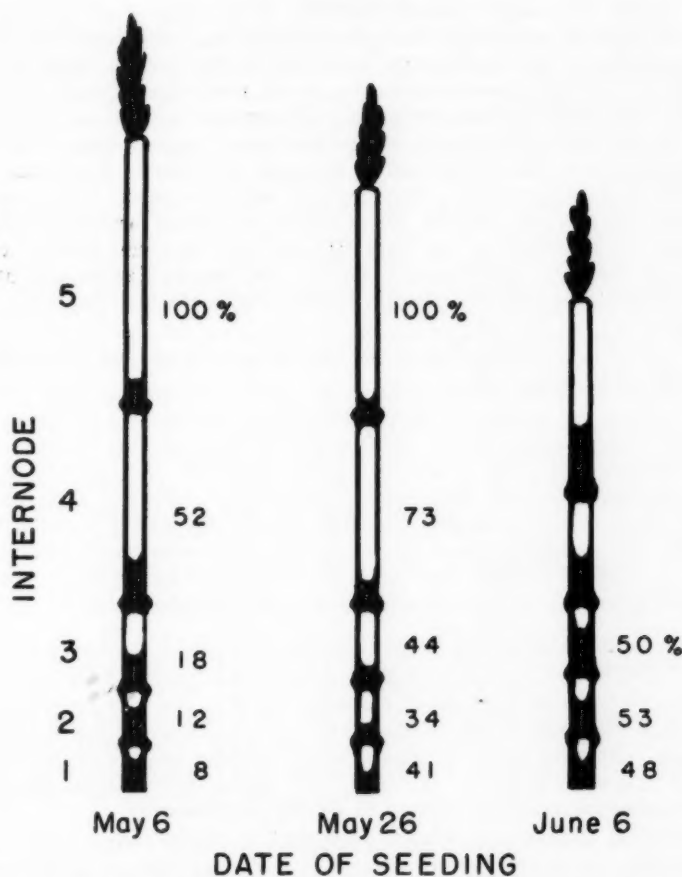


Fig. 3. Average lengths of cavities and the percentages of eggs laid in the cavities of internodes of Rescue seeded on three dates in 1955.

In the later plants more of the eggs were laid in lower internodes. However, in addition to the differences in egg distributions there were differences in stem solidness between dates of seeding as a result of differences in environments. Consequently it may be incorrect to compare the effects of host age on resistance by varying the dates of seeding. Such effects can be determined better by comparisons among internodes of the same stems, although the environments during the development of these internodes do vary.

Fig. 3 shows that the percentages of eggs laid in the cavities of Rescue were progressively higher in the higher internodes of the May 6 seeding in 1955. The cavities were also longer in the higher internodes. The eggs laid in the cavities had greater chances of hatching than those in the pith. Hence, as the stem matured it did not lose its resistance to the eggs but the sawflies changed their oviposition sites to less resistant locations. In these stems 55 per cent of the eggs died. This high mortality resulted from their distribution: 86 per cent were laid in the bottom three internodes, which were mostly solid. Stems of the

May 26 seeding had longer cavities, and only 27 per cent of the eggs in them died. Although 93 per cent of the eggs in this seeding were laid in the bottom three internodes, a high percentage were laid in the cavities because of the increased hollowness of these internodes. In the June 6 seeding, all of the eggs were laid in the bottom three internodes. The cavities in these internodes were fairly long, but although those in Internodes 2 and 3 were shorter than in the May 26 seeding, at least 50 per cent of the eggs were laid in the cavities compared with 34 and 44 per cent in the equivalent internodes of the May 26 seeding. The reason for this was that the plants seeded on June 6 became suitable for oviposition just at the end of the flight (they received just half as many eggs as the May 26 seeding). Internodes 2 and 3 were just starting to elongate and only the upper parts were available for oviposition by the time the sawfly flight had ended.

The percentages of eggs laid in the cavities and the percentages of all eggs in the stems that hatched were:

| | Date seeded | | |
|-----------|-------------|--------|--------|
| | May 6 | May 26 | June 6 |
| In cavity | 18 | 42 | 51 |
| Hatched | 45 | 73 | 81 |

Therefore, the influence of host development on oviposition site is very important in determining the percentages of eggs that hatch in a resistant variety.

It has been shown that age of the stem will shift the oviposition sites and hence give the impression that the plant has lost its resistance to the development of the eggs. Does the stem's resistance to egg hatching actually change with its age at the time of infestation? If it does, then egg mortalities in the pith should change consistently from the bottom to the top internodes.

Infestations in Internode 5 were inadequate to obtain comparisons. However, in Rescue and S-615 the pith showed no consistent differences between the lower four internodes in resistance (Tables II and V). Similarly, as was shown in an earlier section, a consistent change in the mortalities in the pith of Golden Ball did not occur with age of stem at the time of infestation. The age of the stem at the time of oviposition did not determine the differences between internodes in the resistance of the pith to egg survival.

Effects of Various Factors on Hatching of Eggs in the Laboratory

The egg required only air and moisture. Eggs removed from the stems hatched readily on moistened blotting paper. Immersion in distilled water for 16 hours reduced hatching by about 50 per cent, and immersion for 82 hours prevented all eggs from hatching. Eggs resting on water hatched readily. Although five per cent sodium chloride solution applied to blotting paper did not affect hatching, a 10 per cent solution and wheat stem juice applied to the paper reduced hatching by 30 and 60 per cent, respectively. In the wheat juice the development of molds on the eggs appeared to be the major cause of mortality.

Desiccation was the most rapidly acting detrimental factor; after only an hour at room temperature without moisture most eggs collapsed.

Discussion

At least five possible factors may affect the hatching of the eggs in the pith.

The pith may exert a harmful mechanical pressure on the egg. It is unlikely that the female can hollow out a cavity for the egg in pith with the tip of her rigid ovipositor. Possibly the egg itself makes its own cavity by its own turgidity forcing the pith tissues apart. If the pressure of the tissues is too great or if the oviposition cavity is too small the egg may be crushed and killed.

Although the pith tissues at the oviposition site are moist when the egg is laid, they soon lose moisture, and often by the time the egg hatches they appear to be dry. The eggs are very susceptible to drying and if the pith tissues dry out too soon the eggs may die. However, this should occur as frequently in the cavity as in the solid portion. In addition, the durum wheats retain their moisture longer than do the bread wheats, yet egg mortality tends to be greater in the durum than in the bread wheats.

The eggs develop while they are floating on the water, but will not do so if immersed. In the solid part of the internode the egg is surrounded by moist tissue and may even be lying in free moisture. If the tissues remain moist long enough the egg may be killed. The somewhat higher egg mortality in the durum may occur because these wheats retain their moisture longer than do the bread wheats. In support of this hypothesis, at least parts of the eggs laid in the cavities are lying free and even if the tissues remained moist longer than usual the eggs would not be completely immersed and would survive.

The ovipositor undoubtedly carries in microorganisms as it penetrates the stem and also provides an entry for others. This might explain the increased mortality from the increase in numbers of eggs laid in each internode but does not explain the differences in mortalities between the pith and cavity.

The host may produce a toxicant but it appears likely that the parenchyma around the cavity should produce this material as well as the parenchyma in the nearby solid part of the same internode. Hence, there should be no difference in mortalities of eggs in the pith or cavity.

Conclusions

Although some mortality of the egg of the wheat stem sawfly occurred in hollow-stemmed wheats and in the cavities of resistance wheats, most occurred in the pith. The environment in which the internode developed was an important factor as it affected not only the length of cavity available for oviposition but it also influenced the amount of mortality in the pith. Varietal differences also occurred in resistance of the pith to hatching; generally fewer eggs hatched in the pith of Golden Ball than in that of Rescue.

Increases in the number of eggs laid in a resistant stem often resulted in decreased hatching. One reason was that, as the number increased, the percentage laid in the pith also increased. In addition, hatching was higher in the pith of internodes where only one egg was laid than where more than one was laid.

The age of the stems at the time of oviposition did not apparently affect the mortality of the eggs laid in the pith, although it did affect the percentages laid in the various sites, which varied greatly in their effects on the eggs.

The egg was resistant to moderately high osmotic pressures and excesses of moisture but was very susceptible to desiccation and immersion in water. It required only moisture and air to hatch.

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Breeding Behaviour and Oviposition in *Hetaerina americana* (Fabricius) and *H. titia* (Drury) (Odonata: Agriidae)

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Introduction

The objective of this study is to describe the copulatory and ovipositional behaviour of *Hetaerina americana* and *H. titia*, and to depict any differences in such behaviour as may exist between these two species. It is quite important in such studies to understand the mechanisms which assure conspecific mating. Both *americana* and *titia* are found breeding together on many of the streams of central Texas. Williamson (1906) pointed out that species in which the abdominal appendages were very similar often had sexually dimorphic and/or specifically distinct wing coloration, while species with clear wings had quite distinct abdominal appendages. These different wing patterns were suggested as functioning in species recognition for conspecific mating. Buchholtz (1951, 1955) experimentally verified that the females of *Calopteryx splendens* recognize and respond to males of their own species through a set of optical stimuli including the color pattern of the wing. Loibl (1958) and Krieger and Krieger-Loibl (1958) experimentally demonstrated that in *Lestes dryas*, *L. sponsa*, *Ischnura elegans* and *I. pumila*, all of which have clear, colorless wings, the species recognition factors are the shape of the abdominal appendages and body coloration. Williamson's early inferences appear to have been well documented.

Both *Hetaerina americana* and *H. titia* have a striking degree of sexual dimorphism, especially in the coloration of the wings. *H. americana* males have bright ruby-red wing bases and the *americana* females have a diffuse amber coloration in this region. The wings are otherwise clear. *Hetaerina titia* males have the basal red area surrounded by various amounts of brown or black. In extreme cases the whole wing is black with the basal red being much reduced. *Hetaerina titia* females have the wings either clear or diffuse with light brown. One extreme found in the variation of *titia* was earlier treated as a separate species, "tricolor". These wing variations are all figured in Calvert (1901). The inference is therefore made that these different wing patterns play an important part in conspecific mating in *americana* and *titia*.

Buchholtz (1955) also discovered quite different courtship behaviour between populations of the subspecies of *C. splendens*. Much of the status for these subspecies is based on differences in the pattern of wing coloration. These studies show a definite need for more observations on breeding toward revealing adaptation and speciation processes that may go undetected by morphological studies alone.

These observations were made between March 27, 1960 and September 2, 1960. The study sites were the San Marcos River, San Marcos, Texas, and the Colorado River 15 miles west of Austin, Texas, and the San Gabriel River, Georgetown, Texas.

Methods

The observations were all made under natural conditions. The males of the two species are clearly distinguishable and with experience the females can likewise be recognized. The size of these species, 40 to 46 mm., makes it possible to use a 7.5×8 power center focus pair of binoculars. One can therefore select a vantage point and observe accurately throughout a semi-circle of at least a 25 yard radius. Both species prefer streams with ripples where they perch predominantly on exposed overhanging vegetation and debris. The complete period of adult life for most *Hetaerina* is spent in close proximity to these sites, Williamson (1923). Under these conditions *Hetaerina* are very favorable for behaviour studies. Observations were taken on 58 different days for periods of two to four hours each. A total of 68 pairs of *americana* and 28 pairs of *titia* were studied. Simple line drawings are given to illustrate certain phases of the process. Since the reproductive behaviour is very similar for the two species, the wing pattern of the *americana* male is used throughout the Figures. Unless otherwise stated the discussion will refer to both species.

Breeding Behaviour and Oviposition

Both *H. americana* and *H. titia* display a territorial behaviour. The "tricolor" phase of *titia* first appeared on March 30, 1960, and typical *titia* did not appear until May 23, 1960, after which the "tricolor" phase rapidly declined in numbers. The territorial relations and seasonal change in *titia* will be fully presented in a separate paper. The males, as a result of this territoriality, become spaced out along the stream bank on perches generally less than two feet high. The females are predominately found three to six feet from the water's edge and on higher perches.

No precopulatory courtship was ever noted in which both sexes participated. The males however did show a particular characteristic which may function in this respect. From their low perches overhanging the stream the males would frequently fly directly up for about one foot, rapidly beating their wings, and

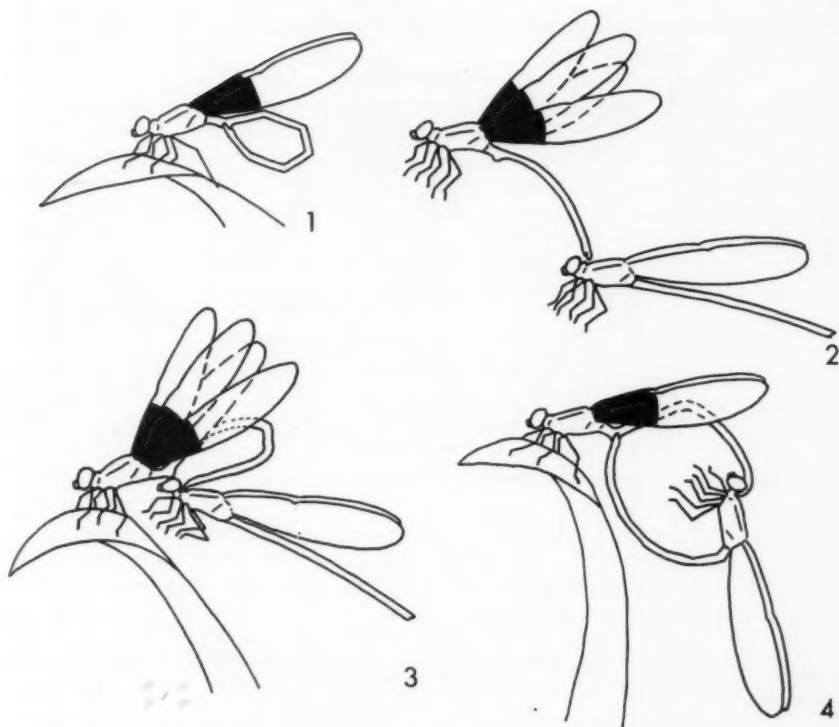
return directly to the same perch. The bright red and brown or black of the wings are exposed to a maximum. These flights were not to obtain food. When food was captured the damselfly would return to its perch and hold the prey between the two front legs while eating it. The flights for food were easily distinguished and occurred mostly when a swarm of small diptera happened by, therefore being quite erratic in timing. The aforementioned flights directly up from and back to the perch were performed in a more regular manner. For 50 *americana* males not otherwise disturbed in territorial behaviour with other individuals, the average interval between such flights was 30 seconds, with a range of 25 to 45 seconds. For 50 "tricolor" males also not otherwise disturbed, the average interval between flights was 90 seconds with a range of 60 to 125 seconds. These counts were all taken from 12 to 4:30 p.m. on the same day on which no overcast was present. At it was impossible to locate a sufficient number of "tricolor" after the appearance of *titia*, I was not able to compare all under similar environmental conditions. However, for 32 *titia* males not otherwise disturbed the average was 45 seconds with a range of 25 to 50 seconds. These figures serve only to emphasize the regularity of these flights in contrast to flights which are a response to other individuals entering the territory, seeking of food or the approach of a predator. One reasonable function of these flights is a display of the presence of a male in the area by displaying the bright wing colors. Such a display could serve a two-fold purpose by deterring the approach of other males and/or announcing the presence of a male to any receptive female. These flights will be referred to as display flights.

The process of copulation will be given after the three steps of odonate copulation of Wesenberg-Lund (1913): 1. The male transfers sperm from the genital pore of the 9th abdominal segment to the penis vesicle located on the venter of the 2nd abdominal segment. 2. The male takes the female in tandem. 3. The female turns her abdomen forward to engage the male's external genitalia, at which time the pair is actually *in copula*.

In both species studied here the male transfers the sperm to the penis vesicle prior to obtaining a mate, as seen in Fig. 1. Buchholtz (1951, 1955) found that European *Calopteryx* did not fill the penis vesicle until after obtaining a female, while the sperm are transferred earlier in populations of the Near East. The temperature increase in the latter area was suggested as an impetus to the sex drive.

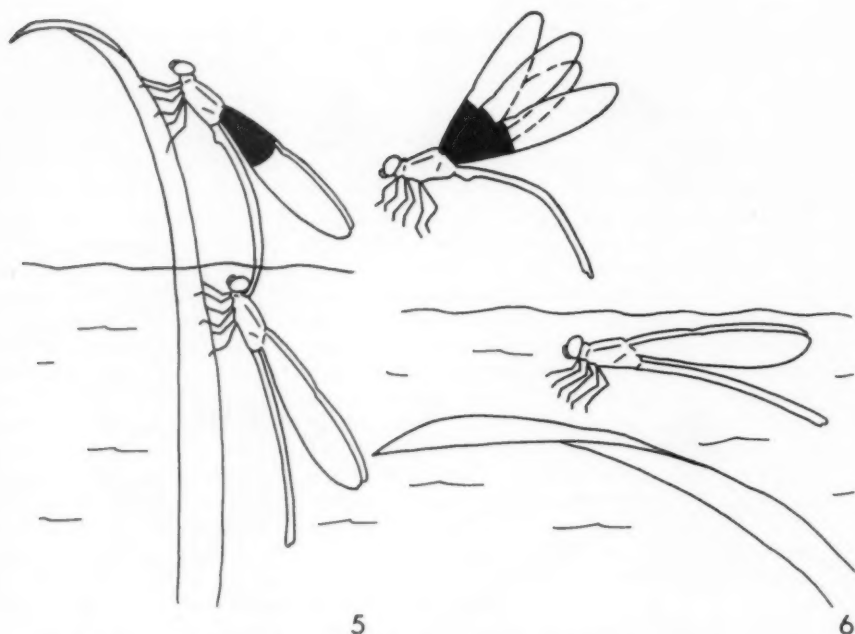
When a female flies into a male's territory the typical territorial response given to other males is not released. The male generally attempts to alight on the female's thorax, however if the female is not receptive she spreads her wings and at the same time bends forward her abdomen. The effect is striking as the male immediately shows no more action toward her. If the female is receptive she flies into the male's territory and appears to hover in one place. The male quickly flies directly to her and attaches his abdominal appendages to the female's prothorax. The whole process is performed in mid air as shown in Fig. 2. The pair then flies off in tandem to a nearby perch within the male's territory. When a female approaches a male in the above manner and he shows her no reaction, it is significant to note that the male in question has a very long-spaced interval between display flights or is a teneral specimen.

The period spent either perched or flying in tandem is quite variable. A pair in tandem attracts aggressive behaviour from neighboring unmated males which have been seen to actually cause a separation of the pair or to displace the pair completely out of sight. When the pair does perch in tandem the male begins a rapid beating of the wings and bends his abdomen upward into a loop. At this



Figs. 1-4. 1. Male transferring sperm to the penis vesicle prior to obtaining a mate. In this and all other Figures the red of the wing base in the male *americana* is shown by shading. The female wings are shown as clear. 2. The male attaches his abdominal appendages to the prothorax of the female, thereby assuming the tandem position in mid air. 3. The dorsal surface of the female's head is struck against the male's external genitalia through a series of pump-like movements of the male's abdomen. 4. The pair in copula.

time the pair is supported only by the male's legs. The male then brings forward his abdomen, carrying the female forward with it, and through a series of jerking movements rubs the dorsal surface of the female's head against his external genitalia, as shown in Fig. 3. The whole procedure is over in a matter of seconds as only five to eight movements are made. This phenomenon was first described by Buchholtz (1951) for *C. splendens*. Its function is not known, however it must serve toward releasing other female responses required for successful breeding. The male then straightens out his abdomen and the female bends her abdomen down and forward to engage the male's external genitalia. Several attempts by the female are often required to successfully go into the copulatory position shown in Fig. 4. The average time spent in copula for *americana* was 3.5 minutes, for "tricolor" was 5.0 minutes, and for typical *titia* was 3.7 minutes. The separation of the pair is preceded by a series of upward movements along the middle segments of the male's abdomen. The pair remains in tandem after the copula is broken. After a two- to six-minute period the pair flies off in tandem for the male to place the female on the oviposition site. The females oviposit completely under water on submerged vegetation of various kinds. The *americana* and typical *titia* males fly out to rapidly flowing water in which sub-



Figs. 5-6. 5. The male places the female on an ovipositing site by walking backward down a perch until the female is completely submerged. 6. The female is dropped into an ovipositing area.

mergent vegetation is growing. If portions of the vegetation project above the surface the male usually alights and proceeds to walk backwards down into the water until the female is completely submerged, as in Fig. 5. The female is then released. When no vegetation projects above the surface the pair flies very low over the water and the female is released to drop into the water, where she sinks down into the vegetation, as in Fig. 6. The male immediately perches on the nearest available foliage or debris and proceeds to drive off other males and any other insects which pass nearby. One such *americana* male was seen to attack and drive off an *Anax junius* which was at least twice its size. This behaviour undoubtedly conforms to a similar phenomenon described by Buchholtz (1951) for *Calopteryx* and termed guarding. Despite many hours of observation I have never seen a female return to the surface. They do descend at least two feet, after which their movements cannot be followed. They proceed slowly with no relation to the direction of the current, ovipositing along the way. Males have been observed guarding up to 40 minutes after placing a female on the site of oviposition. Females encrusted with dried algae have been collected, and other females, alive but obviously exhausted, have been found floating helpless at the water's surface. Buchholtz (1951) gave 30 minutes as a maximum for *C. splendens* to remain submerged. These *Hetaerina* species must remain submerged considerably longer or travel a remarkable horizontal distance.

The "tricolor" phase of *titia* differs in the following ways. The females are placed in still water which is thickly choked with vegetation along the edge of the stream. No *americana* or typical *titia* was ever seen to oviposit in this area. The "tricolor" male remains no more than two to three minutes and then leaves.

No "tricolor" male was ever seen to defend the site where its female was ovipositing.

Discussion

The behavioural sequence of copulation and oviposition has been observed to be the same throughout the season and for the four habitats studied, which included three river drainages. The breeding behaviour is considered to be a genetically determined instinct pattern. The only other record of oviposition in either of these two species was by Kellicott (1899). That author described female *americana* in Ohio as ovipositing with only the abdomen beneath the water's surface. There was no single instance in this study which suggested such a phenomenon. A comparison of northern and southern populations might well reveal a behavioural polymorphism.

Several times a pair which had finished copula and was seeking a site for oviposition was so harassed by non-mated males, often males of both species, that they became separated. Usually the same male is quick in regrasping the female in tandem, however they invariably return to a perch and repeat the whole process of copulation. It appears that before a male will place a female on an ovipositing site they must go through the entire behavioural sequence uninterrupted.

In addition to the male variation in *titia* which gave the basis for "tricolor", the females also differ. In typical *titia* females the mesepisterna of the pterothorax has a metallic green strip bordering the mid-dorsal carina, while "tricolor" has the stripe broken into two elongate but not connecting metallic green spots. Williamson (1912), in synonymizing "tricolor" with *titia* used only males. Calvert (1919) was not able to find intermediates between the two female types. Buchholtz (1956) has shown that differences as small as this do serve as mate recognition between two odonate species. No mention was ever made of which female type was collected in copula with "tricolor" or the typical *titia*. I have collected both female types during this study together in the same habitats, and for pairs collected in copula, the "tricolor" females were always with "tricolor" males and the typical *titia* females were always with the typical *titia* males. The samples are small, however, being 11 "tricolor" and eight *titia* pairs. For the 28 pairs of *titia* observed breeding, seven "tricolor" and five typical *titia* pairs were close enough for a certain identification of the female type to be made. The same relation existed for these as in those given above. There were no intermediates between the female types and no seasonal change in the patterns. Typical *titia* and *americana* males are more similar in respect to the time spent in copula, sites for oviposition, and guarding of the ovipositing female than are "tricolor" and typical *titia* males. The territorial behaviour between "tricolor" and typical *titia* is also quite different, and will be discussed under a separate title. These observations would suggest that closer attention should be given to *titia*.

No non-specific mating was ever observed.

Summary

Four different habitats in central Texas were chosen for observations on the breeding behaviour in *Hetaerina americana* and *H. titia*. Conspecific mating is enhanced through sexually dimorphic and interspecifically different wing coloration patterns. This inference is taken from experimental work where such phenomena were demonstrated for similar Zygoptera.

The males advertise their presence by display flights in which the bright red, black and brown of the wings are exposed to a maximum. Non-receptive

females which enter a male's territory release stimuli which quickly stop all male action toward them. Receptive females which enter a male's territory appear very passive and are taken in tandem in mid air after which the pair perches in the male's territory. The male manipulates its abdomen so as to rub the dorsal surface of the female's head across his external genitalia by several quick movements. The female immediately turns her abdomen downward and forward to engage the male's external genitalia. After three to six minutes the pair breaks the copula. The period spent in tandem varies directly with the number of interfering non-mated males. The male then places the female on the oviposition site where she descends to a depth of at least two feet while ovipositing. All oviposition is done while the female is completely under water. *H. americana* and typical *titia* males guard the area where the female was released. Males of the "tricolor" phase of *titia* do not show the guarding response.

The whole sequence beginning with rubbing the female's head on the male's external genitalia and through copula must be repeated if the pair becomes separated before the male will place a female on the oviposition site.

Several different behavioural characteristics and a seasonal change of abundance between typical *titia* and the "tricolor" phase is noted.

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The Functional Morphology and Interpretation of the Insect Ovipositor*

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Introduction

Elsewhere (Scudder, 1957a), I have outlined briefly a revised interpretation of some basal structures in the insect ovipositor. It was shown that in insects other than the Machilidae, the female genitalia has a common plan, this plan differing from that usually taken as the basic type. Whilst Snodgrass (1933) based his interpretations of all the higher orders on the condition in Machilidae, I have shown that a more satisfactory interpretation is obtained if the condition in the Lepismidae is taken as the basic type.

This paper considers some of the evidence for these conclusions and considers the functional significance and homology of one sclerite, the gonangulum, so important in the new scheme. It is not proposed to consider the homology of the gonocoxae and the gonapophyses, except to state that the evidence available indicates that the former are homologous with pregenital coxae, whilst the latter are probably homologous with eversible sacs present on pregenital segments in Machilidae (Silvestri, 1905; Gustafson, 1950; Scudder, 1957b; Stys, 1959): Matsuda (1957, 1958), however, does not agree with this homology.

The Female Genitalia of *Petrobius maritimus* (Leach)

The two genital segments, abdominal segments VIII and IX (Fig. 1), have typical terga, but the small triangular sterna, present on pregenital segments, are apparently absent. Both segments possess paired gonocoxae (coxae of genital segments) and these bear gonostyli, but eversible sacs are absent. Each gonocoxa also bears an elongate hollow gonapophysis, occupying the position of the eversible sac of pregenital segments.

The Female Genitalia of *Lepisma saccharina* L.

Segment VIII in *Lepisma saccharina*, (Fig. 2) has a typical tergum overlapping ventrally the dorsal part of the first gonocoxa. This gonocoxa on segment VIII, which is shaped like pregenital coxae, bears a gonostyle on its dorsal half posteriorly and a gonapophysis ventrally near the mid-line. Basally this gonapophysis has a membranous connection with the coxa on its outer face. Internally it is attached to the base of an elongate triangular sclerite, the gonangulum. Posteriorly, this gonangulum is attached dorsally to tergum IX, and ventrally to the second gonocoxa. This ventral articulation is with an apparent notch in the second gonocoxa about a third the way along the dorsal surface. The gonostyli of the second gonocoxae are longer than those of the first gonocoxae, and arise in a notch at the apex of the attenuated second gonocoxae. The two pairs of gonapophyses are rather short and do not project far beyond the tips of the second gonostyli.

The female genitalia of *Lepismodes* (= *Thermobia*) *domesticus* (Packard) and *Ctenolepisma quadriseriata* Packard are almost identical with *Lepisma*.

The Female Genitalia in the *Thysanura*: Discussion

The female genitalia of *Petrobius* and *Lepisma* differ fundamentally, in the presence or absence of a gonangulum.

Snodgrass (1935a) incorrectly interpreted the female genitalia of Lepismidae. His drawings (1935a, Fig. G. p. 610) show the gonangulum of *Lepismodes*

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(= *Thermobia*) attached to the second gonapophysis. My work (Fig. 2) and that of Lacaze-Duthiers (1853) show it attached to the first gonapophysis. Snodgrass states that the gonangulum, which he calls the anterior plate (a), is part of the coxae of abdominal segment IX. The apparent notch in the second gonocoxae is also suggestive of such a homology.

The Gonangulum: Its Importance

I have shown (Scudder, 1957a) that this triangular sclerite can be traced in almost all of the higher orders of insects, possessing an ovipositor developed on abdominal segments VIII and IX.

Since the gonangulum is of such wide occurrence it would appear to have been of great selective value; even in some of the most highly evolved insects (e.g. Hymenoptera) the gonangulum is retained and appears to be almost identical functionally and morphologically with that in the Lepismidae. The investigation of the functional significance of the gonangulum also suggests a reason for the apparent conservative modifications of this sclerite.

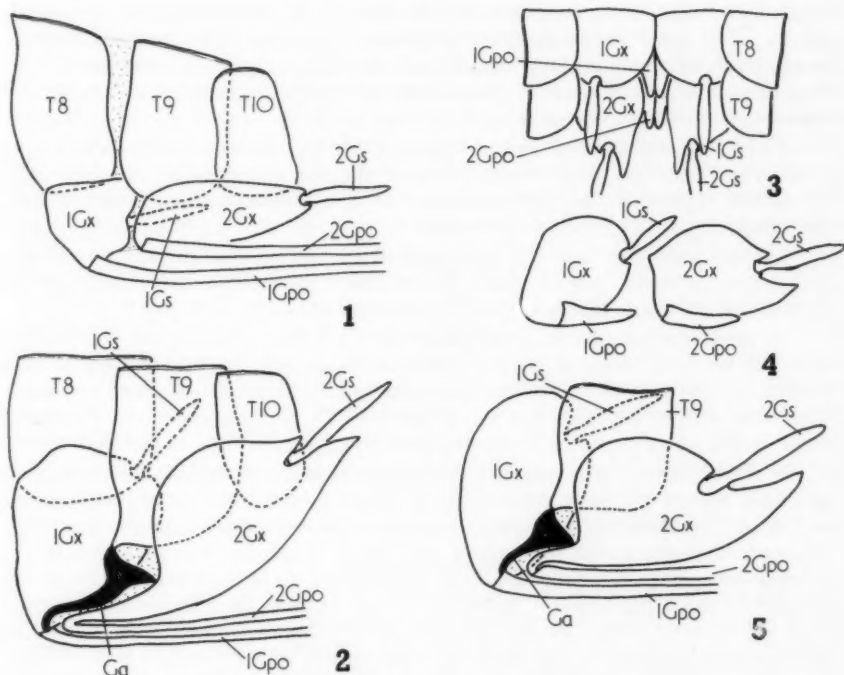
The movements of the ovipositor in many orders has been described by Snodgrass (1933) and reference to his descriptions and figures (1933, p. 140-142, Figs. 48 A & B) of the bee sting shows the mechanics of movement of this organ: similar diagrams show the movements of the ovipositor in other orders. The importance of the gonangulum in these movements cannot be overemphasized. It is possible to build cardboard models of the ovipositor and to show the mechanics and functional importance of the gonangulum in all orders studied. In all it is the most important sclerite, since it is the one structure effecting the movement of the two pairs of gonapophyses relative to each other. In insects which do not oviposit in tissue and so do not have the sawing like motions of the gonapophyses, the gonangulum might be expected to be reduced. This is found in many groups and is well exemplified in the Heteroptera: in the Pentatomidae, Coreidae, and other families which lay eggs on the surface of leaves, bark, etc., one finds the gonangulum weakly sclerotized and sometimes absent altogether, (Scudder, 1959).

Development and Homology of the Gonangulum

The post-embryonic development of the ovipositor in *Lepismodes* (Figs. 3-5) shows that the gonangulum develops from the second gonocoxa as suggested by Snodgrass (1935a). In the earlier instars the genitalia appear almost identical with that found in *Petrobius*. No sign of a gonangulum is present and there is no sclerotized connection between abdominal segments VIII and IX. However, when the insect is about seven millimetres in length, the antero-dorsal corner of the second gonocoxa 'separates' from the rest of the second gonocoxa and connects with the first gonapophysis, tergum IX and the main part of the second gonocoxa, attaining the condition seen in the adult insect.

There can be little doubt that the gonangulum arises from the second gonocoxa in the Lepismidae. In the Exopterygote orders so far investigated, a similar origin is suggested, although the process is not exactly the same as that in Lepismidae. The development of the ovipositor in the Orthopteran *Acheta domesticus* may be taken to illustrate this departure. In the Orthoptera since the adult has the gonangulum fused to the first gonocoxa (Scudder, 1957a), it is to be expected that certain other differences will be found.

In *Acheta*, in the first instar larva, no trace of the ovipositor rudiments are visible, but in the second instar pairs of buds appear at the hind margin of the ninth segment. These are the rudiments of the second gonapophyses and gonoplaques (third gonapophyses of Snodgrass). At the same time a pair of outgrowths



ABBREVIATIONS TO FIGURES

| | |
|-------------|-------------------------------|
| Ga | Gonangulum |
| 1Gpo, 2Gpo | First and second gonapophysis |
| 1Gs, 2Gs | First and second gonostyle |
| 1Gx, 2Gx | First and second gonocoxa |
| T8, T9, T10 | Terga VIII, IX and X |

Fig. 1. *Petrobius maritimus* (Leach)—inner view of skeletal parts of female genitalia of adult.

Fig. 2. *Lepisma saccharina* L.—inner view of skeletal parts of female genitalia of adult.

Figs. 3-5. Development of female genitalia in *Lepismodes domesticus* (Packard): 3, Ventral view of genitalia of early instar female; 4, Inner view of female genitalia of early instar; 5, Inner view of female genitalia of late instar.

develop at the posterior of sternum VIII and later form the first gonapophyses. As the first gonapophyses and gonoplac rudiments develop, at the base of the gonoplacs and just ventral to tergum IX develops a small sclerite, the gonangulum, which Snodgrass (1935b) calls 'x'. Snodgrass states that during the early post-embryonic development there is no evidence of the presence of the gonangulum (= valvifer), except for the small lateral sclerites (x) of the ninth segment, which increase in size and become more dorsal in position. Quadri (1940) also states that on either side of the gonoplacs (= lateral valves) "a small part of the antero-lateral region of the ninth sternum escapes the fate of being absorbed by the growing ovipositor valves of that segment and persists until the final moult when it is fused with the posterior margin of the first pair of valvifers", the first gonocoxae. These gonocoxae are areas of sclerotization that appear laterally to the base of the first gonapophyses. The first gonocoxa is connected to the base of the first gonapophysis and posteriorly has a prolongation which Snodgrass (1935b)

termed 'y', which is inserted between the base of the gonoplares and the gonangulum. The latter gradually becomes closely associated with the ninth tergum. In the adult, the gonangulum (sclerite x) is solidly united with the lobe 'y' of the first gonocoxa and caudally becomes articulated with tergum IX dorsally and the second gonocoxa ventrally.

From the descriptions by Snodgrass (1935b), Quadri (1940) and Gupta (1950), and from my own work, it is clear that the gonangulum develops from the sternal region of the ninth segment. It later develops an articulation with the ninth tergum and second gonocoxa.

Further evidence that the gonangulum is part of the ninth segment and homologous with the gonangulum of Lepismidae is provided by a study of the musculature of these insects (Scudder, unpublished).

A similar origin of the gonangulum as a sclerite appearing on segment IX ventrally or in between segments VIII and IX is seen in the Hemiptera: Stys (1959) regards what I interpret as the gonangulum in the Hemiptera, as merely "a portion of the intersegmental membrane VIII-IX, being secondarily sclerotized between the 1st valvifer and the ventral portion of laterotergite of the IXth urite".

It is well known from many embryological studies that certain developmental processes appear to make short cuts in many animals, in fact in comparative embryology, workers regard such alterations as the rule rather than the exception. The embryologist would not expect the whole sequence of events seen in the development of the female genitalia of *Lepismodes*, to be repeated exactly in the Hemiptera and other orders. Indeed, with reference to specific details, ontogeny does not always recapitulate phylogeny and one may expect variation in specific developmental processes. Studies on the embryology of the Annelids and Molluscs have shown that the ventral nerve cord develops from the ectoderm as two separated latero-ventral longitudinal bands and these come together and meet and fuse in the mid-ventral line (Korschelt, 1936). It is evident that in the insects the origin of the ventral nerve cord is similar, yet we do not find exactly the same process and sequence of events as that in the Annelids: in insects the double nerve cords develop very close to the mid-line and does not result from anlagen migrating mediad from a lateral position (Johanssen & Butt, 1941).

In vertebrates one can call to mind other well known cases of divergence in early embryology, the processes not occurring in all, in the apparent phylogenetic sequence.

In the development of the vertebrate spleen, one finds great diversity in the ontogenetic sequence, yet few would doubt the homology of this organ throughout the phylum. In the Hagfish (Cyclostomes) one finds the spleen represented by dispersed haemopoietic centres in the gut submucosa, in the Lungfish (Dipnoi) these centres are aggregated in the stomach wall, and in the Elasmobranchs, although the spleen arises in the gastro-intestinal tract, during development it moves out and becomes attached to the mesentery (Jordan, 1933). However, in man one finds that at no time are the spleen cells located in the gut. When they do appear, they arise as a localized aggregation of mesodermal cells in the dorsal mesogastrium (Hamilton *et al.*, 1952).

In the salamander and in the chick one also finds differences in the formation of the vertebral column. Whilst notochord plus nerve cord induces skeletogenesis in both, in the salamander membrane bone and cartilage is formed *in situ* in the adjacent somite (Holtzer & Detwiler, 1953; Holtzer *et al.*, 1955), in the chick the somatic cells on induction do not form skeletal tissue *in situ*; the somatic cells migrate from the somite to surround the notochord and nerve cord forming a

loosely packed mesenchyme. Then and then only do they become active in cartilage formation (Hamilton, 1952; Avery *et al.*, 1956).

Finally, in the Amphibia, the development of the optic lens differs according to the species concerned. In all the lens develops from ectoderm overlying the area near the optic cup. In *Rana fusca* the lens forms after contact of ectoderm and optic cup, whereas in *R. palustris* and *R. esculenta*, the lens develops before these two come in contact (see Twitty, 1955). Although this well known case of reinforcing induction is usually used to illustrate another point, namely optic cup plus mesoderm induction in the former and mesoderm induction alone in the latter, it still serves to emphasise the point that the developmental process is not always identical even in fairly closely related species.

That such ontogenetic differences have a genetic basis is indicated by the work of Schotté (1930) and Spemann & Schotté (1932).

Thus it is scientifically sound to regard the gonangulum in the Exopterygote insects as homologous with that in *Lepisma*: no satisfactory account of the development of the gonangulum in the Endopterygote orders is available, but work is in progress on this.

If the above homology of the gonangulum in the Insecta is accepted, and the available evidence suggests that it should be, then a new interpretation of the ovipositor in many of the orders is inevitable: this will be considered elsewhere.

Acknowledgments

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Predators of Larvae of *Neodiprion swainei* Midd. (Hymenoptera: Tenthredinidae)¹

By W. A. SMIRNOFF²

In 1958, *Pilophorus ubleri* (Knight) (Hemiptera: Miridae), *Vespula vulgaris* (L.) and *V. rufa consobrina* (Sauss.) (Hymenoptera: Vespidae) were recorded for the first time as being not only active predators of *Neodiprion swainei* larvae, but also vectors of a virus disease affecting this sawfly (Smirnoff, 1959). The latter vespid was considered to be especially important. In the summer of 1959, in the same area (St. David de Falardeau, Lake St. John region, Que.), more insect species were identified, which preyed on the first- and second-instar larvae of *N. swainei*. Most active were *Lasioglossum (Euclyptus)* sp. (Hymenoptera: Halictidae) and *Crabro* sp. (Hymenoptera: Sphecidae), while three species of *Vespula* were also observed: *V. maculata* (L.), *V. arenaria* (Fab.) and *V. norvegica norvegicoides* (Slad.) (Figs. 1-4). This completes the list of insects which have been observed to prey on *swainei* larvae. Data were also obtained on the period of greatest activity of each of these predators.

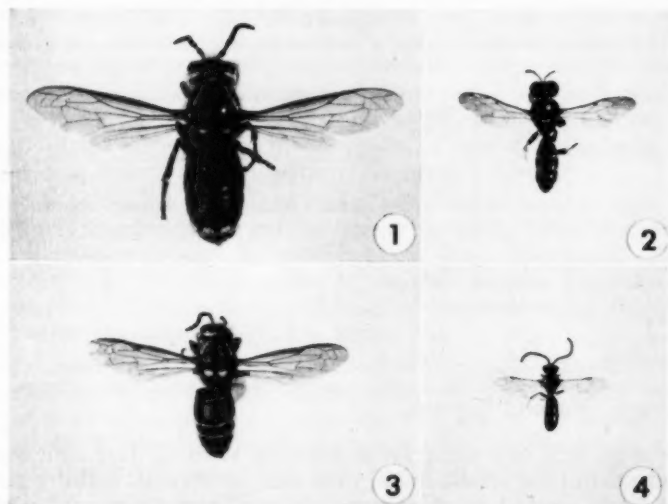
Methods

Part of a small jack pine stand infested by *N. swainei* during the last four years was placed under observation. The study trees were of medium size, thinly scattered, and located in the centre of a large field. The study area also included the border of another stand located on the northwestern side of the same field.

Preliminary studies of the factors governing the numbers of *P. ubleri* and their area of distribution were undertaken during the period of greatest abundance of each *swainei* larval instar. Sampling consisted in shaking the tree tops over a piece of white cloth and the insects falling on the cloth were afterwards

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Figs. 1-4. Predators of *N. swainei* larvae. 1, *Vespula maculata*. 2, *Crabro* sp. 3, *Vespula rufa consobrina*. 4, *Lasioglossum* sp.

collected by means of an ordinary aspirator, to be used for further studies. For the *Vespula* and the other species of Hymenoptera, the method was as follows: Estimates of the number of insects hovering above *N. swainei* colonies were made every second or third day, on the basis of samples obtained with a net. During the course of the investigations the feeding and flight habits of the predacious species were closely observed.

General Observations on Predators of *N. swainei* Larvae

In the summer of 1959, owing to a sudden rise in temperature, a mass hatching of *N. swainei* eggs occurred on July 12, 10 to 15 days earlier than in the previous year. Observations made four days prior to the hatching of the sawfly eggs established that *P. ubleri* settled exclusively upon those pine trees which carried egg clusters of *N. swainei*. At that time, up to 70 per cent of the *P. ubleri* population was still in the immature, nymphal stage, but with the development of *N. swainei* larvae to first instar, *P. ubleri* reached the adult stage everywhere and the estimated total number of specimens averaged 26 per tree. Towards the end of July, *P. ubleri* became less numerous, and the average number of specimens per tree went down to 12; this number decreased further when *N. swainei* larvae reached the third instar and finally *P. ubleri* disappeared completely.

Another species of Hemiptera, *Platylygus luridus* (Reut.), was found on pine trees infested by *N. swainei*, as well as on healthy trees, but its predatory behaviour has not yet been investigated.

On July 16, for the first time, large numbers of *Lasioglossum* (*Evylaeus*) sp. were noticed hovering above branches bearing first-instar larvae of *N. swainei*. Further observations showed that these insects had a marked preference for *N. swainei* colonies located on the sunlit side of the trees in the forest border adjoining the field. *Lasioglossum* usually hovered in groups of some 20 to 30 individuals, at a distance of 10 to 20 cm. above the colonies of *N. swainei* larvae.

The insects first circled about for a few minutes, before one of them pounced upon a sawfly larva and flew away with it in the direction of the field. These

TABLE I
Relation between the various species of predators and the larval instars of *N. swainei*

| Species of predators | Length in mm. | Wing span in mm. | Abundance of predators with regards to larval instars and size of larvae of <i>N. swainei</i> | | | | |
|--|---------------------|---------------------------|---|------------|-------------|-------------|------------|
| | | | I 3mm. | II 5mm. | III 9mm. | IV 14mm. | V 18mm. |
| <i>Lasioglossum</i> sp. | 7.5 | 11.3 | †† | †† | — | — | — |
| <i>Crabro</i> sp. | 11.0 | 17.0 | — | † | — | †† | — |
| <i>Vespula vulgaris</i> | 12.5 | 20.0 | — | — | †† | — | † |
| <i>Vespula arenaria</i> | 12.0 | 21.5 | — | — | — | — | — |
| <i>Vespula rufa</i> <i>consobrina</i> | 15.0 | 22.0 | — | — | — | †† | †† |
| <i>Vespula maculata</i> | 19.5 | 31.0 | — | — | — | † | †† |

Legend:—scarce; †average; ††numerous

predators were especially active for a period of 10 to 12 days until the sawfly larvae had reached the second instar; then their numbers dwindled rapidly, and when the larvae reached the third instar, the predators disappeared completely.

About the time the sawfly larvae were reaching their third instar, another predacious insect, *Crabro* sp., appeared, but in much lesser numbers than *Lasioglossum*. It differed further from the latter by flying above the colonies of sawfly larvae singly or sometimes in pairs, rather than as groups. When most of the colonies of *N. swainei* larvae had reached the third instar, the attacks of *Crabro* were no longer observed.

By the end of July three species of vespids made their appearance, in the following order: *Vespula norvegica norvegicoides* (Slad.), *V. arenaria* (Fab.), and *V. vulgaris* (L.). The numbers of the first two species did not increase during the summer, but the population of *V. vulgaris* increased rapidly up to August 15 and only then began to decline. *V. rufa consobrina* appeared at the beginning of August when *N. swainei* larvae were in the third and fourth instars. They became numerous and hovered above *N. swainei* colonies up to the end of August and into September. In the middle of August, *V. rufa consobrina* was joined by *V. maculata*, a predator of importance but less numerous than the former. Both of these species remained active up to the time when *N. swainei* larvae started to spin their cocoons.

TABLE II
Predators attacking *N. swainei* colonies

| Species of predators | Period of observation and larval instar dominant | | | | |
|--|--|---------------------|---------------------------------|-----------------------|----------------------|
| | 17-20 July I | 21-26 July II | 29-31 July 1-5 August III | 10-17 August IV | 24-29 August V |
| <i>Lasioglossum</i> sp. | †† | †† | — | — | — |
| <i>Crabro</i> sp. | — | † | — | — | — |
| <i>Vespula vulgaris</i> | — | — | †† | †† | † |
| <i>Vespula arenaria</i> | — | — | — | — | — |
| <i>Vespula norvegica norvegicoides</i> | — | — | — | — | — |
| <i>Vespula rufa consobrina</i> | — | — | — | †† | †† |
| <i>Vespula maculata</i> | — | — | — | † | †† |

Legend:—scarce; † average; ††numerous

The systematic sampling of the associated insect fauna provided a basis for determining the period of predominance of particular species of predators. Table I gives the results of such computations; the data are presented separately for each larval instar of *N. swainei*, at the time when it was predominant in the field. Measurements are also included on the average width of wing span and the length of the body of each of the predators, as well as the body length of the larvae used as food by each species.

The predominance of different species of predators depends upon the instar reached by *N. swainei* larvae and the size of the sawfly larvae is a determining factor, for upon it depends the ability of each predacious species to seize and carry off its prey. This is supported by the data listed in Table II, pertaining to the different periods of activity of the various predators during the corresponding stage of development of the sawfly larvae.

The fact that *N. swainei* larvae are attacked by predators during their periodic outbreaks illustrates the faculties of adaptation which characterize some of the local species of entomophagous and polyphagous insects. It appears that such an adaptability is related to the great numbers of *N. swainei* infesting the same locations during several consecutive years as well as to other favourable circumstances.

Larvae weakened by hunger, migration, parasitism or disease may lose the faculty for spontaneous protective movements at the approach of other insects and thus become an easy prey for predators. For instance, the introduction of a virus disease of *swainei* in the region about two years ago was reflected in a rapid increase of the number of predators and an extension of their activity, especially in the case of many species of *Vespula*. Long before death occurs, the larvae, when infected by the virus, become torpid and may be unable to resist attacks by predacious insects.

Acknowledgments

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The Distribution and Abundance of Wireworms in the Annapolis Valley of Nova Scotia¹

By C. J. S. Fox

Introduction

The Annapolis Valley is about 100 miles long and is one of the largest and most important of the agricultural areas of the province. The general relief is undulating to gently rolling, with general slopes from the North and South Mountains to the Annapolis and Cornwallis Rivers. The soils of the Annapolis Valley and Hants County were described by Harlow and Whiteside (6) and Cann, Hilchey and Smith (1). A wireworm survey was conducted between 1951 and 1958 since it was suspected that economically important species of European wireworms, namely *Agriotes sputator* (L.), *A. obscurus* (L.), and *A. lineatus* (L.), which occur elsewhere in the province, might be invading the area. The results of this survey are reported here.

Methods

Two hundred and twenty-eight fields were surveyed in Kings County, 48 in Annapolis County, and 23 in Hants County between 1951 and 1958, a field being defined as an area of at least one acre, of apparently uniform soil type and that had been uniformly subjected to cultural practices.

The sampling unit was a block of soil six inches square at the top and eight inches deep as suggested by Ladell (7). Over 98 per cent of the larvae are included in samples taken to this depth. One such sample was taken at random in each quarter of an acre. Every sample was numbered and recorded so that the point of sampling could be relocated if desired. In suitable weather, the samples of soil were examined outdoors by sifting through a sieve of one-quarter or one-sixth inch mesh screen onto a square of canvas. The larvae were picked up from the thin layers of sifted soil and their numbers recorded. In inclement weather, the samples were taken to the laboratory, and, if too wet, were allowed to drain before screening. By this method nearly all wireworms over three mm. long were collected. Larvae that could not be identified to species were reared individually in jars at about 66°F. to obtain adults for identification.

The date, locality, soil type, cropping history of the field, number, genus or species of adults and larvae, and the number of pupae collected were recorded for each sample. The publications of Harlow and Whiteside (6) and Cann *et al.* (1) were followed in describing soil type.

The wireworm survey became partly advisory in purpose. This introduced a bias in that numerous fields were surveyed at the request of growers who knew or suspected that wireworms were present.

Results and Discussion

The genera of wireworms identified and their prevalence in different textural classes is given in Table 1. The differences in average numbers per acre were found to be statistically significant indicating a positive relationship between soil texture and population density. Differences could not, however, be demonstrated between soil series within textural classes. The highest wireworm populations were found in the dikelands. Here larvae of *Dalopius pallidus* and *Ctenicera cylindriciformis* were more numerous and those of *Agriotes* less numerous than on other soil types. The next highest populations were found in muck and the silty North and South Mountain soils, followed by soils of clay and sandy parent

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TABLE I

The occurrence of several genera of wireworm in the various common textural classes of soil of the Annapolis Valley

| | Textural classes of soil | | | | | | | | | |
|---------------------------------|--------------------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|
| | Dikeland | | Muck | | Silt | | Clay | | Sand | |
| | Num- ber | % of total | Num- ber | % of total | Num- ber | % of total | Num- ber | % of total | Num- ber | % of total |
| <i>Agriotes</i> | 73 | 30.8 | 45 | 95.8 | 651 | 79.7 | 703 | 85.5 | 889 | 76.4 |
| <i>Hypolithus</i> | 14 | 5.9 | 0 | 0 | 77 | 9.4 | 44 | 5.4 | 90 | 7.7 |
| <i>Ctenicera</i> | 57 | 24.0 | 1 | 2.1 | 68 | 8.3 | 48 | 5.8 | 119 | 10.2 |
| <i>Dalopius</i> | 91 | 38.3 | 1 | 2.1 | 12 | 1.5 | 10 | 1.2 | 22 | 1.9 |
| <i>Oestodes</i> | 1 | 0.5 | 0 | 0 | 0 | 0 | 10 | 1.2 | 22 | 1.9 |
| Others | 1 | 0.5 | 0 | 0 | 9 | 1.1 | 7 | 0.9 | 22 | 1.9 |
| Total | 237 | | 47 | | 817 | | 822 | | 1164 | |
| Number of sampling units | 218 | | 60 | | 1131 | | 1184 | | 1820 | |
| Average number (1000's/acre) | 189 | | 136 | | 126 | | 121 | | 111 | |

materials. Thus, in general, the populations were greater as the fineness of the soils increased, probably because of good soil fertility and high water capacity, and hence favorable vegetation.

Grouping the fields according to the average pH of the soil gave no indication that this factor of itself influenced the numbers of wireworms. This is in accord with the findings of Gui and Malik (5), MacLeod and Rawlins (8), and Ladell (7). In this connection it is of interest that although *Limonius aeger* Lec. occurs in the muck soils of Ontario and Quebec it was not collected in the more acid muck soils of the Annapolis Valley but has been occasionally collected near forested areas not included in the present survey.

Populations as low as one larva per square foot (approximately 44,000 per acre) may cause considerable damage to a potato crop and approximately two-thirds of the fields examined had populations exceeding this density.

Table 2 shows that in general the longer a field was in grass the higher the wireworm population. However, observations outside the surveyed area, in districts infested by the European species, *A. sputator*, showed that old and badly deteriorated grasslands had relatively low populations. The age groups used here for the grass fields were chosen because farmers and farm workers appeared to remember readily the age of grassland when it was less than four years old and were usually able to say with certainty that a given field had been in grass for over ten years but ages between were often difficult to determine accurately.

TABLE II

The numbers of wireworms on grasslands of different ages

| | Age of grassland (years) | | |
|-------------------------------|--------------------------|-----|-------------|
| | 1-3 | 4-9 | 10 and over |
| Number of fields surveyed | 54 | 65 | 65 |
| Average numbers (1000's/acre) | 58 | 119 | 233 |

TABLE III
The numbers of wireworms in relation to years of continuous cultivation

| | Number of years cultivated | | | |
|-------------------------------|----------------------------|-----|----|------------|
| | 1 | 2 | 3 | 4 and over |
| Number of fields surveyed | 32 | 17 | 11 | 24 |
| Average numbers (1000's/acre) | 208 | 199 | 94 | 78 |

Table 3 shows the influence of repeated annual cultivation on larval populations in fields where the number of years under cultivation was known. The data support the general observation that the numbers of wireworms decline when grassland is cultivated and the decline continues as long as the fields are cultivated, as was also noted by Roebuck (9). The decline is attributed chiefly to the removal of comparatively dense ground cover and hence attractive ovipositing sites (3, 4), but mechanical injury by implements, exposure to predators, and desiccation probably caused high mortality.

Annotated List of Species Collected

Aeolus mellilus (Say) (flat wireworm)—Several larvae were recovered from fields near Wilmot and Bridgetown, Annapolis County. In the laboratory, they died on a wheat diet. It has not previously been reported in Canada east of Ontario.

Agriotes mancus (Say) (wheat wireworm)—The most abundant and injurious species in the surveyed area except in dikelands where *Dalopius pallidus* Brown was dominant. Apparently especially attracted to low, wet heavy soils as it was most numerous in muck and in soils of clay parent material. Readily reared on a vegetable diet.

Agriotes sputator (L.)—A severe infestation of this European species was found near Round Hill, Annapolis County. A serious pest in grassland and cultivated fields near Digby and Sydney, N.S. This species may become a serious pest in the Annapolis Valley but forested areas bar its spreading. In contrast to *A. mancus* it is often numerous in high, rather dry grassland.

Athous affinis Couper—Probably an European introduction as it is known only from Granby, Quebec, and from Digby, Annapolis Royal and Sweet's Corner, N.S. It is not known to be of economic importance. Nine larvae were collected near Annapolis Royal and were successfully reared on a diet of wheat. In the laboratory this species feeds readily on smaller wireworms so may be of importance as a predator.

Ctenicera cylindriciformis Herbst.—Found throughout the surveyed area, often associated with *A. mancus* but it is not numerous in cultivated fields. Most numerous in dikeland, indicating a preference for low, wet land. It may be partly carnivorous (2) as in the laboratory only 18 of 330 larvae matured on a diet of wheat.

Dalopius pallidus Brown—The dominant species in dikeland and is rare in well-drained fields. It has been seen feeding on potatoes and turnips.

Hemicrepidius memnonius Herbst.—This large species was rarely collected from poorly drained areas of fields. Often numerous in piles of rotting leaves, and is readily reared on a diet of wheat.

Hypolithus abbreviatus Say—This species is less injurious to potatoes than *A. mancus* with which it is often associated, as it does not tunnel deeply, nevertheless, it is an important pest. About 40 per cent of attempted rearings on wheat were successful.

Melanotus spp.—Only 23 specimens of this genus were found during the survey. In the laboratory one was successfully reared on a wheat diet and identified as *M. castanipes* Payk; seven are still alive.

Oestodes tenuicollis Rand—This species was rarely found and only in bottom-land. Larvae could not be reared on a vegetable diet and it was not observed to injure plants. Not previously reported from Nova Scotia.

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Records and Descriptions of North American Species in the Genus *Lepidostoma*, with a Revision of the *Vernalis* Group (Trichoptera: Lepidostomatidae)

By O. S. FLINT, JR.¹, AND G. B. WIGGINS²

In the course of our studies of the Trichoptera of the southern Appalachians during the past few years, considerable material of the genus *Lepidostoma* has been accumulated. In addition to range extensions and previously undescribed females in various groups within the genus, this material has provided four new species in the *vernalis* group. With the number of species in this group thus doubled, we believe it useful to provide here a revision of the whole *vernalis* group, with keys to the males and females. Knowledge of the immature stages is not adequate to permit any systematic analysis at this time.

The holotypes and allotypes of the new species are deposited in the United States National Museum. Paratypes are distributed among the collections of the Royal Ontario Museum, the Illinois Natural History Survey, and the senior author.

Vernalis Group

Heretofore, this was a group of five species. In this study, however, four new species are added, and the recently described *carrolli* Flint is transferred to it, making ten in all. As far as we know, representatives of this group are confined to eastern North America.

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Adults of the *vernalis* group may be recognized by the prominent dorsal warts on the terminal abdominal segments. These warts bear a patch of hairs, but these break off readily, particularly in specimens preserved in alcohol, and specimens are often encountered in which the hairs have almost entirely disappeared. The males bear a pair of these warts on each of the sixth, seventh, eighth and ninth segments. The warts on the females are smaller than those on the males, and somewhat variable in different species. Warts are always present on at least the ninth segment of the females (Fig. 14b), and they are not reduced to an irregular row of setae as in some of the other groups (Fig. 11b).

Like most of the other species of *Lepidostoma*, adults of the *vernalis* group are uniform brown in colour. Secondary sexual modifications, common in this genus, are confined in most of these species to differences in the maxillary palpi. In the females the palpi are composed of the five normal slender segments, but in the males the maxillary palpi are reduced to what appears to be a single, rather long segment. This is flattened, and curved dorsad rather close to the face. In males of only one species, *griseum*, are there any additional modifications, and these are described under that species.

Several terms employed in the keys and descriptions throughout this paper may require some clarification. On the dorsal surface of the clasper in all the males of the *vernalis* group is a finger-like lobe, usually flattened dorsoventrally, known as the dorsal process. In lateral view the apical portion of this dorsal process is separate from the main body of the clasper. At the base of the clasper there is usually a sclerotized process, more or less vertical, and variously shaped as a low plate, a hook, or a long point in different species. The aedeagus has an internal sclerite which differs markedly in shape in different species. In the females of the *vernalis* group the ninth and tenth tergites are considerably modified. The ninth is roughly triangular with the apex produced into a flap-like process which may be divided. The tenth tergite is divided mesally, with the two halves deflected ventrad. The sternum of the eighth segment forms the subgenital plate, on which the sclerotized areas are often weakly delimited. These areas are most clearly made out before the specimen is cleared in KOH. The posterolateral margins of the subgenital plate are sometimes extended as thin sclerotized flaps. The apex of the plate is generally trilobate, but in some species the apex is membranous and difficult to make out clearly. Internally, there is the heavily sclerotized, ovoid spermatheca, which in ventral aspect has a central keyhole-like opening. The spermatheca is attached by membranous connections to the apex of the subgenital plate, and when these connections are sclerotized, they are referred to as lateral bands. The lateral bands are not as well developed in the *vernalis* group as in some of the others. Arising at each side of the spermatheca is a narrow sclerotized strap, the ventral bridge, which extends across the ventral surface and is more or less angulate in the middle.

Key to Males of the *vernalis* Group

1. Dorsum of the ninth segment enormously enlarged and bulbous, overhanging all other parts of the genitalia (Fig. 10) *sackeni*
- Dorsum of the ninth segment not enlarged, the whole segment in the form of a fairly regular ring (Fig. 7) 2
2. Base of the clasper with a long, heavily sclerotized process which terminates in a single sharp point (Figs. 1, 3) 3
- Base of the clasper with a shorter sclerotized process which is hooked (Fig. 5), fork-like (Fig. 4), or quadrate (Figs. 7, 8) 5
3. Sclerotized process at the base of the clasper strongly recurved, the apical portion nearly parallel with the main body axis (Fig. 1) *liba*

- Sclerotized process at the base of the clasper long and straight, the apical portion extending from the main body axis at an angle of about 45° (Figs. 2, 3) 4
4. Clasper deep in lateral view; lateral processes of the tenth segment in dorsal view parallel, mesal processes dentate (Fig. 3) *stylifer*
Clasper narrower in lateral view; lateral processes of the tenth segment in dorsal view divergent, mesal processes smooth and not dentate (Fig. 2) *mitchelli*
5. Sclerotized process at the base of the clasper fork-like (Fig. 4), or hook-like (Figs. 5, 6) in lateral view 6
Sclerotized process at the base of the clasper more or less quadrate in lateral view (Figs. 7, 8, 9) 8
6. Tenth segment consisting of a pair of very heavily sclerotized, pointed, hook-like mesal processes, and a pair of shorter and somewhat less heavily sclerotized lateral processes; sclerotized process at the base of the clasper fork-like (Fig. 4) *vernalis*
Tenth segment consisting of a pair of moderately sclerotized, club-like lateral processes and mesal membranous folds; sclerotized process at the base of the clasper hook-like in lateral view (Figs. 5, 6) 7
7. Apex of the clasper with a deep notch; sclerotized process at the base of the clasper fairly straight, its long axis parallel to the long axis of the body and thus seen in full profile in lateral view (Fig. 6) *excavatum*
Apex of the clasper without a deep notch; sclerotized process at the base of the clasper curved, its full profile visible only in posteroventral view (Fig. 5) *sommermanae*
8. Tenth segment circular in lateral view, with two short, sclerotized, ventral processes, each bearing an apical spine (Fig. 9) *griseum*
Tenth segment not circular in lateral view 9
9. Tenth segment consisting mainly of two stout lateral processes, their dorsolateral edges with deep serrations (Fig. 7) *serratum*
Tenth segment consisting of an overhanging dorsal plate, the margins variously produced into small points (Fig. 8) *carrolli*

Key to Females of the *vernalis* Group³

1. Ninth tergite sharply bilobed apically (Fig. 14b) *sackeni*
Ninth tergite no more than slightly emarginate apically 2
2. Genitalia with an internal bilobed plate, extending beyond the apex of subgenital plate (Fig. 15) *carrolli*
Genitalia lacking any internal plate that extends beyond subgenital plate 3
3. Posterolateral margin of subgenital plate with a wide, convex flap (Fig. 16) *mitchelli*
Posterolateral margin of subgenital plate without any flap, or with a narrow, concave one 4
4. Posterolateral margin of subgenital plate with a narrow, concave flap (Fig. 22) 5
Posterolateral margin of subgenital plate without a thin flap 6
5. Apex of subgenital plate membranous; lateral bands of spermatheca with a pair of apical parenthesis-like marks, and a pair of lateral, elongate marks (Fig. 17) *serratum*
Apical lobe of subgenital plate sclerotized and more distinct; lateral bands of spermatheca with inner margins darkened apically (Fig. 22) *excavatum*
6. Lateral bands of the spermatheca dark laterally, becoming paler mesally; ventral bridge of spermatheca nearly straight, body of spermatheca subequal in length and width (Fig. 19) *griseum*
Lateral bands of spermatheca marked differently; ventral bridge nearly right-angled at midline, spermatheca elongated 7
7. Apical lobes of subgenital plate membranous; lateral bands of spermatheca divided by a longitudinal, dark line, darkened laterally (Fig. 20) *vernalis*
Apical lobes of subgenital plate sclerotized; lateral bands of spermatheca not darkened laterally 8
8. Lateral lobes of subgenital plate heavily sclerotized, with a dark internal line; lateral bands of spermatheca indistinct (Fig. 18) *liba*
Lateral lobes of subgenital plate only slightly sclerotized; lateral bands of spermatheca with internal borders heavily sclerotized (Fig. 21) *sommermanae*

Lepidostoma vernalis (Banks)

Mormonia vernalis Banks, 1897, p. 29.

Mormomyia vernalis Banks, 1907, p. 127; Ulmer, 1907, pl. 13, fig. 117, pl. 14, fig. 118; Sibley, 1926, p. 106; Betten, 1934, p. 401.

³The female of one species, *L. stylifer*, is not yet known.

Lepidostoma vernalis Ross, 1938, p. 44, fig. 90; Ross, 1946, p. 287; Denning, 1949, p. 122; Morse and Blickle, 1953, p. 101.

Male (Fig. 4). Length of fore wing 9 mm. Maxillary palpi one-segmented, flattened, curved dorsad rather close to the face and about the same length as the scape. Readily distinguished from the other species by the hook-like processes of the tenth segment.

Ninth segment broadened dorsally, the dorsal warts large. Clasper rectangular in lateral view, with the apex truncate and toothed, and bearing a rounded mesal lobe; dorsal process long in lateral view, with a heavily sclerotized basal prong which is divided apically, somewhat like a fork. Aedeagus with a pair of elongate sclerites united and widened at the base. Tenth segment in lateral view consisting of a sharply pointed, but rather short, lateral process, and a long, very heavily sclerotized, mesal process; in dorsal view these two processes appear as the opposing ends of a single hook-like process.

Female (Fig. 20). Similar in general structure to the male; distinguished from females of the other species by the membranous apex and sides of the subgenital plate, and by the well-marked lateral bands of the spermatheca which are conspicuously darker laterally.

Ninth tergite terminates mesally as a rounded lobe. Subgenital plate weakly sclerotized, apex indistinct. Lateral bands of spermatheca distinct, with a longitudinal median division laterad of which they are heavily sclerotized. Ventral bridge of spermatheca with the median angle nearly 90 degrees.

Material Examined. *Massachusetts.* State Fish Hatchery, Sunderland: 1 ♂, V-11-55; 1 ♂, V-20-55; 1 ♂, VII-30-54. *Michigan.* Sanborn Cr., Nirvana (record per H. H. Ross). *New York.* Ellis Hollow, Town of Dryden: many ♂ and ♀, VI-9-56; VII-8-56. McLean: 2 ♂, V-29-59. Montauk, L. I. (record per H. H. Ross). *Ontario.* Whitney: 3 ♂ 2 ♀, VII-8-59. Leskard: 3 ♂, VI-16-53; 2 ♂ 1 ♀, V-21-55.

Range and Habits. This species has been recorded from Massachusetts, New Hampshire, New York and now Ontario. Banks (1914) recorded the species from Tryon, North Carolina, but we have examined this specimen in the Museum of Comparative Zoology and find that it is not *vernalis*, but probably *mittelli*. Further comment on this specimen will be found in the section concerning that species. Betten (1934) records and describes *vernalis* from New York, but his figures (pl. 62, figs. 8, 9) are of *sommermanae*. Sibley (1926) also records this species from New York. The species does occur at McLean, N.Y., and collections made by both Betten and Sibley, and now in the Cornell University collection, contain a mixture of both *vernalis* and *sommermanae*.

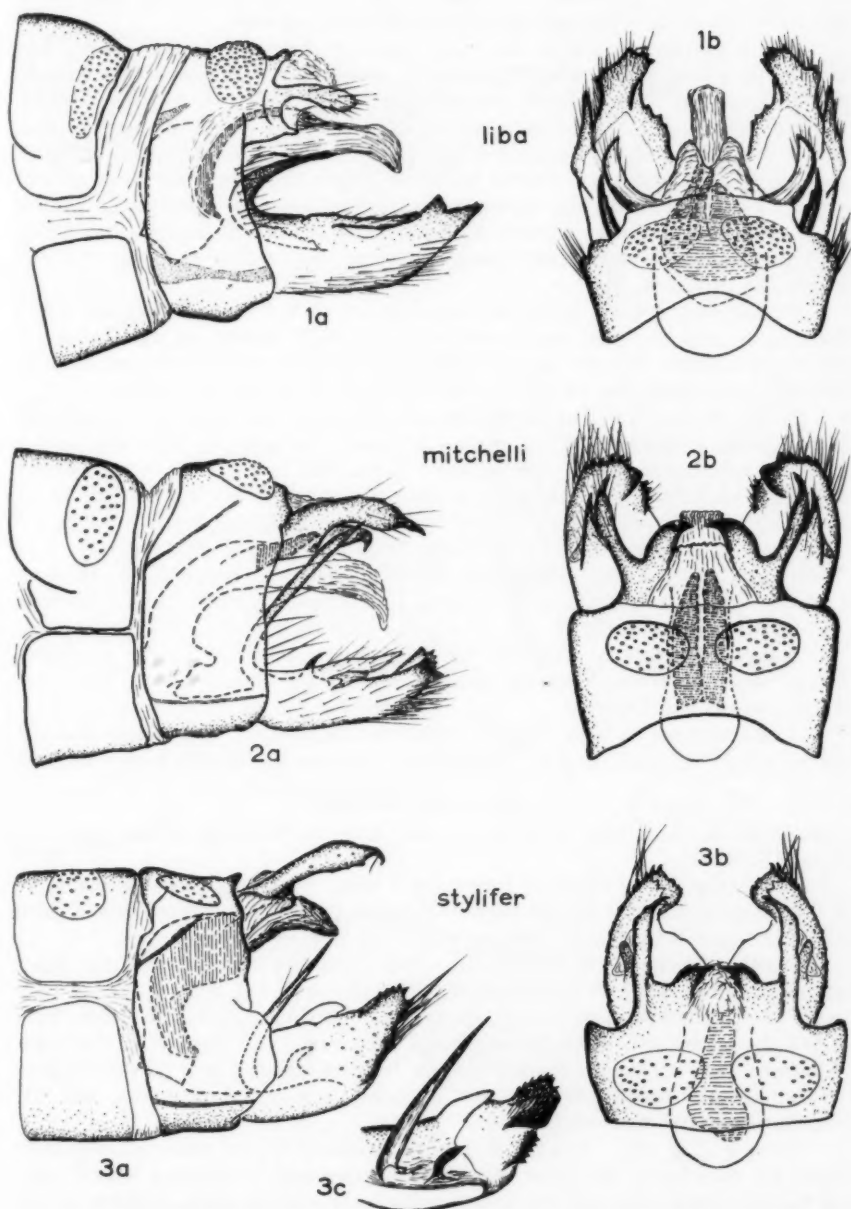
All our collections of this species have been made beside small, spring-fed streams, and presumably these streams are the larval habitat. The adults are often found during the day resting in crevices on the bark of trees near these streams, where they are so well camouflaged that only rarely does one see them before they fly. Adults of this species are primarily vernal, although we have taken them in numbers in July at Dryden, New York. Banks (1897) records the adults as common along the streams in March, April and May on Long Island, New York.

Lepidostoma sackeni (Banks)

Mormontia sackeni Banks, 1936, p. 267, fig. 9.

Lepidostoma sackeni Ross, 1946, pp. 287-88, fig. 19; Morse and Blickle, 1953, p. 101.

Male (Fig. 10). Length of fore wing 7 mm. Maxillary palpi consisting of a single segment, flattened and curved dorsad as in *vernalis*. Antennae, wings



Figs. 1-3. Male genitalia and terminal abdominal segments of *Lepidostoma* spp., a, lateral view; b, dorsal view; c, mesal surface of clasper, lateral view. 1, *L. liba*; 2, *L. mitchelli*; 3, *L. styliifer*.

and legs without modifications. Very readily distinguished from the other species by the greatly enlarged dorsum of the ninth segment.

Ninth segment somewhat narrowed ventrally, but the dorsum greatly enlarged into a crest which extends posteriorly well beyond the genital appendages; this crest consists of two inflated, peanut-shaped lobes, with a ventral membranous portion; the dorsal warts of the ninth segment are situated on the anterior end of the crest, the hairs of the warts lying along the dorsum of the crest. Clasper short and deep, the apex divided into two finger-like lobes, the apex of the ventral lobe turned sharply mesad; posteroventral edge of the clasper with a small mesal point. Aedeagus with a rounded sclerite. Tenth segment consisting of a pair of heavily sclerotized plates, each one terminating in a pair of stout finger-like processes.

Female (Fig. 14). Similar in general structure to the male. Distinguished from females of the other species by the apical bifid process on the dorsum of the ninth segment, by the lateral shelf-like lobes and unusual sclerotization of the subgenital plate, and by the twisted lateral bands of the spermatheca.

Ninth tergite extended posteriorly as a sharply bifid process. Subgenital plate weakly sclerotized in two parts — a roughly rectangular basal area, and a bilobate apical area; apical sclerotization sometimes indistinct; a posterolateral shelf-like extension on each side of the subgenital plate. Lateral bands of spermatheca dark and twisted; ventral bridge of spermatheca nearly straight.

Material Examined. *Massachusetts.* Paradise Brook, Sunderland: 2♂, VIII-28-56. *New York.* Wildflower Preserve, Slaterville Springs: 1♀, IX-4-56. *Ontario.* Black Ash Creek, Collingwood Township: 1♀, VIII-21-48. Kendal: 1♂ 1♀, IX-11-53. Leskard: 1♂, IX-13-52. Oro Station: 1♂, VIII-15-52.

Range and Habits. This species is apparently confined to the northeast, being recorded from New Hampshire, New York, Pennsylvania, and now Massachusetts and Ontario.

The adults are in flight during August and September. It is likely that the larvae live in the small, cold streams beside which the adults have been collected.

Lepidostoma liba Ross

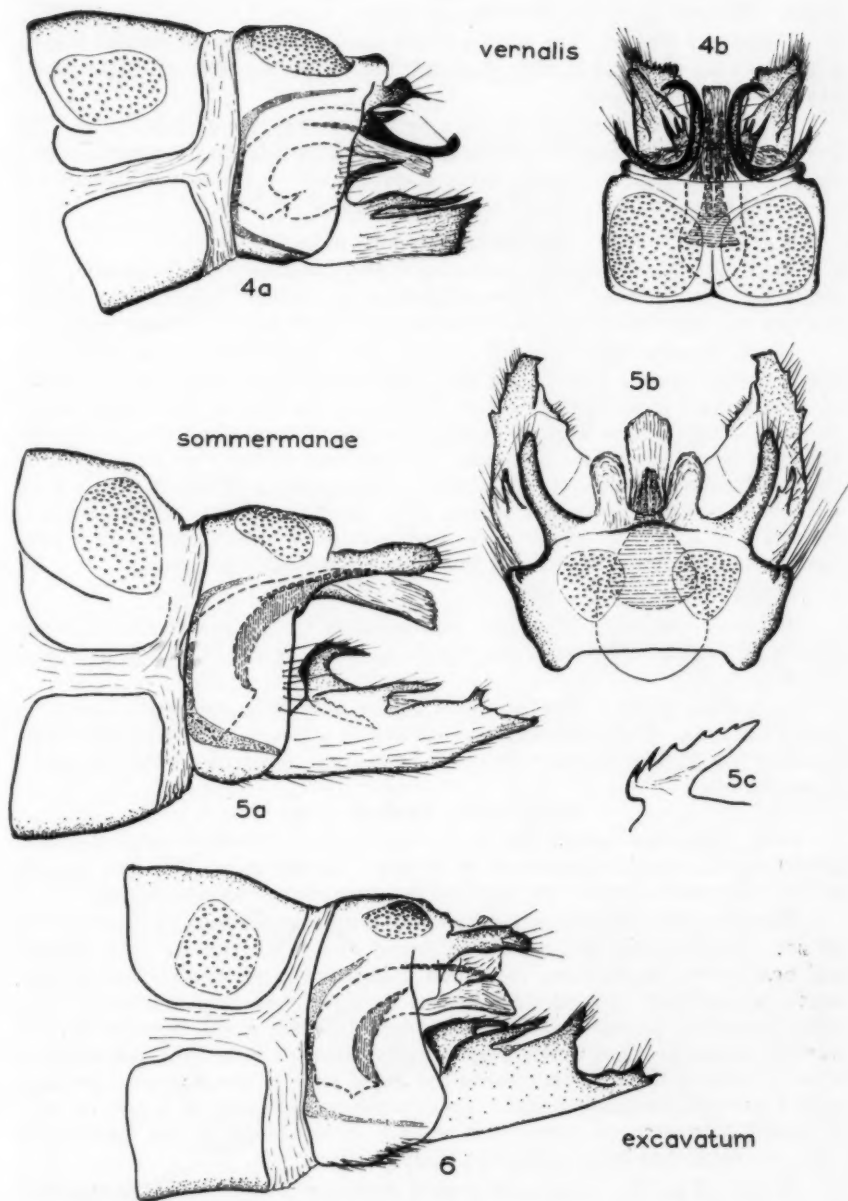
Lepidostoma liba Ross, 1941, p. 120, fig. 97; Ross, 1944, pp. 259-60, figs. 882-84; Ross, 1946, p. 287, fig. 33.

Male (Fig. 1). Length of fore wing 7 mm. Maxillary palpi consisting of a single segment, flattened, and curved dorsad as in *vernalis*. Distinguished from the other species by the recurved prong at the base of the clasper.

Ninth segment fairly uniform in width, confluent dorsally with the tenth segment; dorsal warts of moderate size. Clasper long, the apex in lateral view with two large teeth; dorsal process long and finger-like; base of the clasper with a heavily sclerotized, stout prong, sharply recurved, and pointed at the apex. Aedeagus with a broad, irregular sclerite, terminating in a pair of slender processes. Tenth segment with a pair of lateral sclerotized processes, and the intervening mesal area membranous.

Female (Fig. 18). Similar in general structure to the male; distinguished from the females of the other species by the strongly sclerotized lateral lobes of the subgenital plate and the almost completely membranous condition of the lateral bands of the spermatheca.

Ninth tergite projecting apically as a truncate lobe. Subgenital plate rather uniformly sclerotized, lateral lobes very strongly sclerotized and complex, the inner portions showing through the subgenital plate. Lateral bands of spermatheca indistinct; ventral bridge obtusely angled at midline.



Figs. 4-6. Male genitalia and terminal abdominal segments of *Lepidostoma* spp., a, lateral view; b, dorsal view; c, posteroventral view of process at the base of the clasper. 4, *L. vernalis*; 5, *L. sommermanae*; 6, *L. excavatum*.

Material Examined. *Illinois.* Elgin Botanical Gardens, Elgin: 2 ♀, VI-20-46. Gulfport: 1 ♂ 1 ♀, IX-9-39.

Range and Habits. The species is still not known to occur outside Illinois. The adults are recorded in May, June and September, suggesting a flight period like that of *sommermanae*.

The habits were discussed by Ross in 1944, and are summarized here. The larvae are found in spring-fed brooklets. The youngest larvae construct a round, sand-grain case, but the mature larvae construct the typical square case of leaf pieces. The larvae were also described and figured by Ross.

***Lepidostoma stylifer* n. sp.**

Male (Fig. 3). Length of fore wing 8 mm. Maxillary palpi consisting of a single segment, flattened and curved dorsad as in *vernalis*. Closest to *mittelli*, but can be readily distinguished by the deeper clasper with its narrow apex.

Ninth segment fairly regular in width, the dorsal warts of moderate size. Clasper rather deep in lateral view, the apex narrowed and finger-like, consisting of two dentate lobes, the dorsal one obscuring the ventral one when viewed dorsally; dorsal process short, originating somewhat mesad and thus partly obscured in lateral view; base of clasper extended into a long, pointed process; on the mesal edge of each deeply concave clasper arises a short, sharply pointed sclerotized process. Aedeagus with a large irregular sclerite. Tenth segment consisting of a pair of heavily sclerotized, divided processes, each with a long, fairly straight, pointed lateral arm, and a short, mesal, dentate lobe.

Female. Unknown.

Material Examined. *Holotype, male:* Indian Gap, about 5,000 ft., Great Smoky Mountains National Park, North Carolina, VII-1-58 (Flint and J. F. Hanson).

Range and Habits. This species is known only from the single locality in North Carolina. The specimen was captured at a lantern placed beside a small tumbling brook, near the point where it crosses a trail, not far from the foundation of an old hotel.

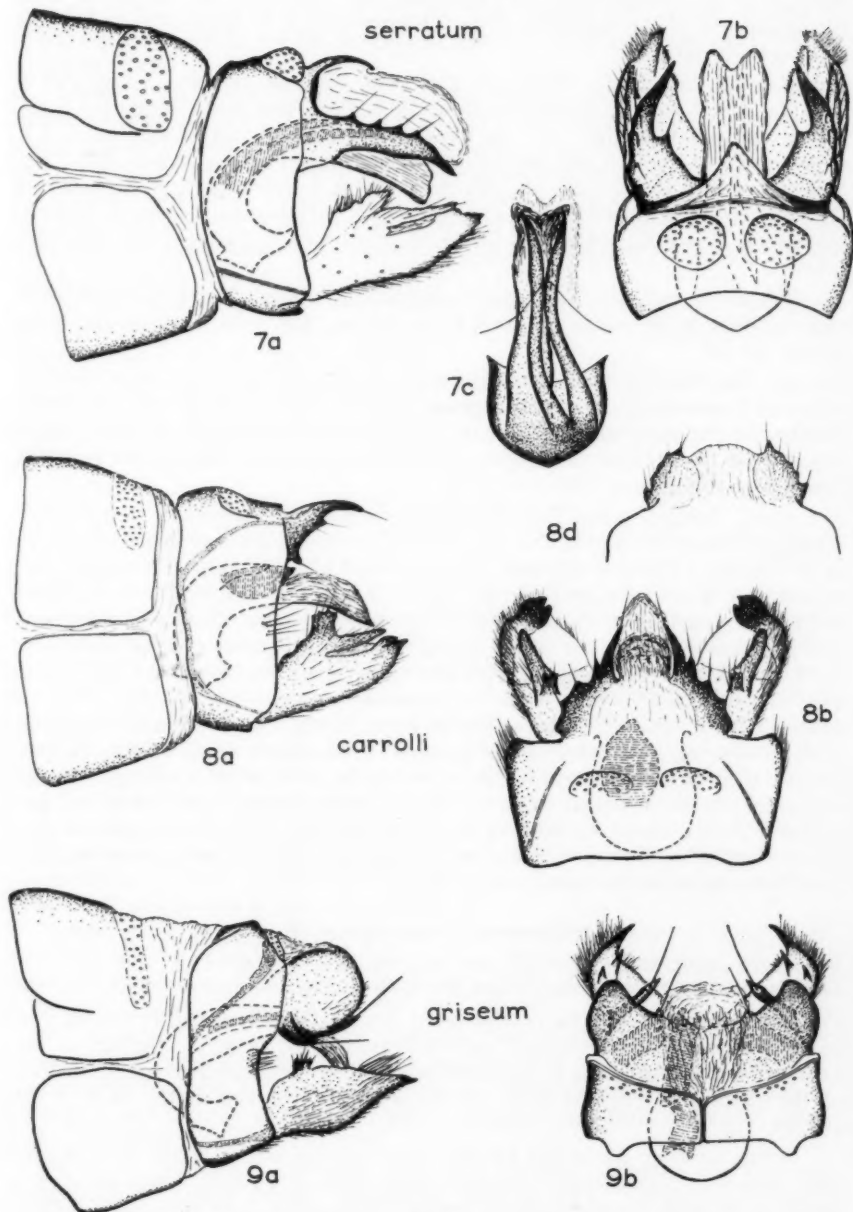
***Lepidostoma mittelli* n. sp.**

Male (Fig. 2). Length of fore wing 8 mm. Maxillary palpi flattened, consisting of a single segment as in *vernalis*. Closest to another new species, *stylifer*, but can be readily distinguished by the narrow, truncate clasper.

Ninth segment of fairly uniform width throughout, the dorsal warts moderate in size. Clasper long and narrow in lateral view, the truncate apex dentate, and bearing two mesal lobes, the dorsal lobe smooth, the ventral lobe dentate; dorsal process long in lateral view; base of the clasper extended into a very long, thin, sclerotized process which reaches dorsad to the tenth segment; a small pointed process lies on the mesal edge of each clasper near the base, and, in lateral view, projects a short distance above the dorsal edge of the clasper. Aedeagus with a pair of elongate sclerites. Tenth segment consisting of a pair of stout Y-shaped processes, the longer arm of each directed laterad, the shorter arm directed mesad, and both ending in a sharp point.

Female (Fig. 16). Similar in general structure to the male. Distinguished from the other species by the large posterolateral, flap-like expansions of the subgenital plate.

Ninth tergite projects apically as a truncate lobe. Apical portion of the subgenital plate with two ovoid sclerotized plates, each sclerotized plate projecting posterolaterally as a thin convex ledge; mesal lobe well sclerotized.



Figs. 7-9. Male genitalia and terminal abdominal segments of *Lepidostoma* spp., a, lateral view; b, dorsal view; c, aedeagus and processes, dorsal view. 7, *L. serratum*; 8, *L. carrolli* (8a and b — specimen from Sunset, Deer Isle, Maine; 8d — tenth segment, dorsal view, paratype from Lakehurst, N.J.); 9, *L. griseum*.

Margins of the lateral bands well delimited, the inner margin continuous with the apical lobe of the subgenital plate. Ventral bridge of spermatheca with the median angle obtuse.

Material Examined. *Holotype*, male and *allotype*, female: Camp Alice, 5796 ft., Mt. Mitchell, North Carolina, IX-16-58 (Flint and Wiggins). *Paratypes*: Same locality, but 1 ♀ pupa collected IX-1-59, emerged IX-2-59; 1 ♂ 2 ♀ pupae collected IX-3-59, emerged IX-7-59, 1 pupa preserved (Flint and Wiggins). Stream crossing Route 128, Mt. Mitchell, North Carolina, 1 ♂ pupa collected IX-1-59, emerged IX-59 (Flint and Wiggins). Highlands Biological Station, Highlands, North Carolina, 1 ♀, IX-14-58 (Flint and Wiggins). See also note below.

Range and Habits. This species is known only from North Carolina, with two localities at elevations of 4,000 ft. or more. The adults are on the wing during the fall.

On Mt. Mitchell the larvae inhabit small streams, from two to three feet wide, and consisting of alternate pools and cascades. The pupae are found attached to the undersurface of rocks. The cases are associated with, and indistinguishable from, those of *griseum*, but the latter is from fifty to one hundred times more abundant in our collections.

Note. A single male in the Banks collection in the Museum of Comparative Zoology, collected at Tryon, N.C. by W. F. Fiske, was identified by Banks (1914) as *L. vernalis*. We have examined this specimen and it does not belong to that species, but is most similar to *L. mitchelli*. There are, however, certain differences in the genitalia between this Tryon specimen and our material, and without additional specimens we are unable to evaluate the significance of these variations. For the present we are assigning this specimen to the new species *mitchelli*, and any male specimens of this type which are subsequently found will emerge as *mitchelli* with this key. The specimen from Tryon differs from our material in the following characters: dorsal portion of the ninth segment considerably broader than the ventral portion, the warts on the dorsum twice as large; clasper somewhat deeper in lateral view, the basal process shorter and thicker and not reaching the dorsolateral process of the tenth segment; apex of the clasper wider; mesal tooth of each clasper absent; tenth segment with the mesal processes considerably ventrad of the dorsolateral processes.

Lepidostoma sommermanae Ross

Mormomyia vernalis Betten (*nec* Banks), 1934, p. 401, pl. 62, figs. 8, 9.

Lepidostoma sommermanae Ross, 1946, pp. 286-87, figs. 18, 34.

Male (Fig. 5). Length of fore wing 7 mm. Maxillary palpi consisting of a single segment, flattened, and curved dorsad as in *vernal*is. Similar to *excavatum*, but distinguished from that species by the more regularly tapered apex of the clasper, and by the shape of the sclerotized process at the base of the clasper.

Ninth segment somewhat broader dorsally, the dorsal warts of moderate size. Clasper elongate in lateral view, tapering toward the apex, with a prominent dorsal tooth near the apex; dorsal process fairly short; base of clasper with a stout, heavily sclerotized, dentate process, the main axis of which is largely at right angles to the body axis, although in lateral view the pointed apex of this process is curved laterad to appear as a prominent hook. Aedeagus with a broad sclerite, terminating in a pair of slender processes. Tenth segment with a pair of sclerotized lateral processes, and a mesal membranous portion.

Female (Fig. 21). Similar in general structure to the male. Distinguished from the females of the other species by the heavily sclerotized central projection of the subgenital plate, and by the conspicuous dark line on the lateral bands of the spermatheca.

Ninth tergite projecting apically as a truncate or slightly emarginate shelf. Subgenital plate with a purse-shaped sclerotized area mesally; apical lobe especially well sclerotized. Inner margins of lateral bands of spermatheca delimited by a distinct line; ventral bridge of spermatheca angled at nearly 90 degrees mesally.

Material Examined. *Massachusetts.* State Fish Hatchery, Sunderland: 28 ♂ 24 ♀, VI-1 to X-15-54; 1 ♀ pupa, VIII-28-56. *Virginia.* Shenandoah National Park, Big Meadows Camp Ground: larvae, III-27-56, reared to adults. White Oak Canyon trail: 1 ♂, IX-18-58.

Range and Habits. The species was recorded from Connecticut, New York and Pennsylvania in the original description. Massachusetts and Virginia can now be added to the known distribution.

The adults were collected throughout the summer, from the first of June to mid-October, in Sunderland, Massachusetts. Ross (1946) reported the larvae from a small, spring-fed brooklet, where they made round cases of sand grains. All our observations are in complete agreement.

Lepidostoma excavatum n. sp.

Male (Fig. 6). Length of fore wing 7 mm. Maxillary palpi consisting of a single segment, flattened, and curved dorsad as in *vernalis*. Similar to *sommermanae*, but distinguished from that species by the deep excavation in the apex of the clasper, and by the shape of the sclerotized process at the base of the clasper.

Ninth segment somewhat broader dorsally, the dorsal warts of moderate size. Clasper appearing rather short in lateral view, largely because of the deep excavation near the apex, with a prominent tooth at each apical corner; dorsal process somewhat longer than in *sommermanae*; base of clasper with a stout, heavily sclerotized, dentate process as in *sommermanae*, but the main axis of this process is largely parallel to the main axis of the body, and not at right angles to the body axis as in *sommermanae*; in lateral view, then, the full profile of this basal process is apparent, rather than only part of it as in *sommermanae*. Aedeagus with broad sclerite terminating in a pair of slender processes as in *sommermanae*. Tenth segment with a pair of lateral sclerotized processes and a mesal membranous area as in *sommermanae*.

Female (Fig. 22). Similar in general structure to the male. Distinguished from the females of the other species by the distinct posterolateral shelf-like expansion of the subgenital plate, and by the sclerotized apex of the lateral band of the spermatheca.

Ninth tergite with apical lobe truncate. Subgenital plate with a narrow, concave, shelf-like projection along each posterolateral margin; apico-mesal projection well sclerotized, lateral lobes less so. Lateral bands of spermatheca indistinct, marked only at apices; ventral bridge of spermatheca nearly right-angled at midline.

Material Examined. *Holotype, male* and *allotype, female*: Indian Gap, about 5,000 ft., Great Smoky Mountains National Park, Tennessee, IX-13-58 (Flint and Wiggins). *Paratypes*: same data, 2 ♂ 3 ♀. See also note below.

Range and Habits. The species has been taken only in Tennessee and North Carolina at high elevations. It is apparently a fall-flying species.

The males were collected at a gasoline lantern, the females by sweeping vegetation, alongside a small spring-fed brooklet. Although the larva has not

been reared, this brooklet and adjacent springs contain an abundance of *Lepidostoma* larvae in round, sand-grain cases which are probably of this species.

Note. A single male collected at Crabtree Meadows Camp Ground, Blue Ridge Parkway, North Carolina, IX-3-59, is not included in the type series because it shows some variations. The apex of the clasper is not as deeply excavate as in the type series, and the specimen tends to approach *sommermanae* in this character. The dentate process at the base of the clasper is smaller than in the type series but the main axis of this process is still parallel to the main axis of the body. On the strength of this character, this specimen is here assigned to *excavatum*. It does give an indication, though, that other intermediates between typical *excavatum* and *sommermanae* may occur, and that speciation within the complex may still be under way.

***Lepidostoma griseum* (Banks)**

Phanopsyche grisea Banks, 1911, p. 357, pl. 12, figs. 17, 19, 22; Sibley, 1926, pp. 106, 212, pl. 9, figs. 45-53; Carpenter, 1933, p. 36, fig. 17; Betten, 1934, pp. 407-08, pl. 64, figs. 6-12. *Lepidostoma griseum* Ross, 1946, p. 286, figs. 17, 32; Denning, 1949, p. 120; Morse and Blick'e, 1953, p. 101.

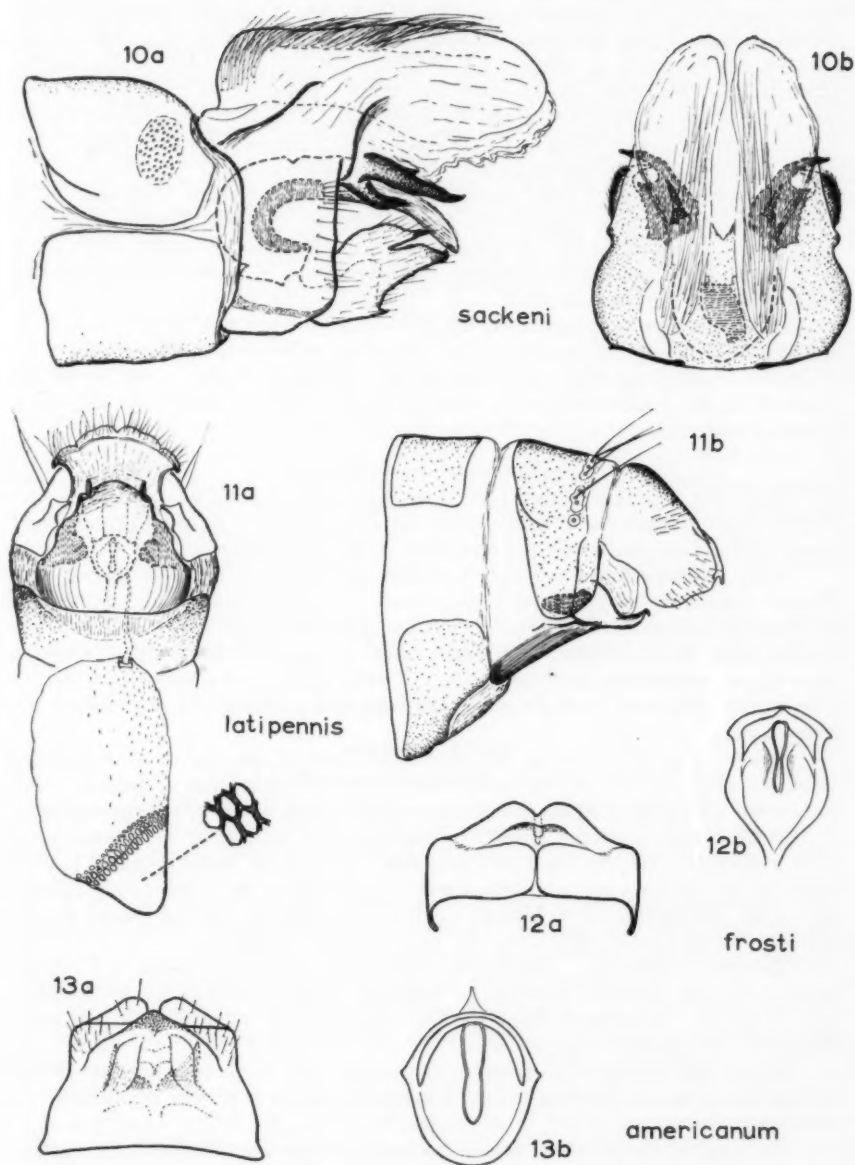
Male (Fig. 9). Length of fore wing 8 mm. Maxillary palpi different from those of the other species in the group, flattened and sharply elbowed in the middle, the distal arm directed dorsad, and a thick brush of hairs at the angle. Warts of the mesoscutum and mesoscutellum with thickened hairs. Hind wing with a prominent arcuate ridge, formed by two right-angled folds, extending from the origin of the wing to the apex of R_4 ; hind wing with extensive patches of short thick hairs. Dorsal warts on the abdomen narrow. Readily distinguished from the other species by the hood-like structure of the tenth segment.

Ninth segment fairly regular in width, the dorsal warts narrow. Clasper elliptical in shape in lateral view, the apex with a sharp point directed mesad; in dorsal view two other pointed mesal lobes can be seen, the upper one of these probably representing the dorsal process of other species; base of clasper with a dorsal truncate lobe, which in caudal view is seen to be an elongate sclerotized plate. Aedeagus with an irregular, elongate sclerite. Tenth segment appearing in lateral view as a heavily sclerotized spherical lobe with two stout ventral prongs; in dorsal view it appears as a pair of sclerotized dorsal plates, each with the lateral edges rolled under, their apical points extended mesad as stout processes.

Female (Fig. 19). Similar in general structure to the male, but without the ridge in the hind wing, and without thickened hairs on that wing and on the mesonotum; distinguished from the other species by the trilobed apex of the subgenital plate, and by the distinct lateral bands and truncate apex of the spermatheca.

Ninth tergite terminates apically as a rounded lobe. Subgenital plate strongly sclerotized on the apical half; apicomeral and apicolateral projections also strongly sclerotized, although somewhat less so in specimens from the more northern parts of the range. Spermatheca rather short, the posterior margin somewhat truncate; lateral bands well developed, dark laterally, paler mesad; ventral bridge with the median angle very wide.

Material examined. Georgia. Black Rock Mountain State Park, Rabun Co.: 2 ♂ 2 ♀, IX-12-58. Maine. Sunset, Deer Isle: 9 ♂, VIII-19-59; 10 ♂ 2 ♀, VIII-20-59; 8 ♂, VIII-26-59. Massachusetts. Sunderland: 1 ♂ 3 ♀, VIII-28-56. New Jersey. Lakehurst: 1 ♂ 2 ♀, IX-6-55. New York. Cortland Fish Hatchery, Cortland: larvae, VII-8-59, later reared to adults. North Carolina. Highlands



Figs. 10-13. Genitalia and terminal abdominal segments of *Lepidostoma* spp. 10, *L. sackeni* male, 10a lateral view, 10b dorsal view; 11, *L. latipennis* female, 11a ventral view, 11b lateral view; 12, *L. frosti* female, 12a ninth and tenth segments, dorsal view, 12b spermatheca, ventral view; 13, *L. americanum* female, 13a ninth and tenth segments, dorsal view, 13b spermatheca, ventral view.

Biological Station, Highlands: 1 ♂ 1 ♀, VIII-23-58; 3 ♂ 7 ♀, IX-2 to IX-14-58. Five miles south of Highlands: 1 ♂ 1 ♀, IX-10-58. Crabtree Meadows Camp Ground, Blue Ridge Parkway: larvae, male and female pupae, VIII-31 to IX-2-59, later reared to adults; 1 ♂, VIII-31-59; 1 ♂, IX-2-59. Camp Alice, 5,789 ft., Mt. Mitchell: larvae, male and female pupae, IX-1 to IX-3-59 later reared to adults. Bridal Veil Falls, Watauga Co., VIII-6-48 (record per H. H. Ross). Ontario. Oro Station: 1 ♂, VIII-15-52. Virginia. Skyline Drive, Mile Post 71.5, Shenandoah National Park: 1 ♂ pupa, IX-11-57.

Range and Habits. This species has been recorded from Michigan, New Hampshire, New Jersey, New York, North Carolina, Ontario, Pennsylvania, and Tennessee. Georgia, Maine, Massachusetts, and Virginia are added to this list.

Adults of this species are common and widespread in eastern North America during August and September.

The larvae live in springs or small, cold, clear streams that generally contain an abundance of organic matter. The case is square in cross-section and is made of leaf or bark fragments, as is typical for the genus. The pupal cases are attached to the under surfaces of rocks or sticks. Sibley (1926) has described the larva and pupa.

***Lepidostoma serratum* n. sp.**

Male (Fig. 7). Length of fore wing 7 mm. Maxillary palpi consisting of a single segment, flattened and curved dorsad as in *vernalis*. Readily distinguished from all the other species by the structure of the tenth segment.

Ninth segment fairly uniform in width, the dorsal warts of moderate size. Clasper somewhat elliptical in lateral view, narrowed toward the apex, and terminating in a slender, dentate lobe; dorsal process fairly long; base of clasper with a low, vertical ridge. Aedeagus with a pair of long pointed arm-like appendages, originating asymmetrically. Tenth segment consisting of a pair of long serrate processes, each broad at the base and tapering sharply toward the pointed apex.

Female (Fig. 17). Similar in general structure to the male. Distinguished from the other species by the posterolateral extensions of the subgenital plate, and by the pair of parenthesis-like marks on the lateral bands of the spermatheca.

Ninth tergite truncate apically. Posterolateral margin of subgenital plate with a narrow, concave shelf on each side; apical lobe membranous. Lateral bands of spermatheca apically with a pair of parenthesis-like marks, and laterally with dark, elongate marks. Ventral bridge of spermatheca tending to be drawn out indistinctly posteriorly; obliquely angulate near middle.

Material Examined. *Holotype*, male and *allotype*, female: Crabtree Meadows Camp Ground, Blue Ridge Parkway, North Carolina, IX-16-58 (Flint and Wiggins). *Paratypes*: Same locality, but IX-3-59, 1 ♀; IX-2-59, 1 ♂ pupa (Flint and Wiggins).

Range and Habits. *L. serratum* is known only from one locality in the mountains of North Carolina. This species, like many others in the group, is a fall-flying form.

The single male pupa was found in a large seepage area, on the under surface of a stick. The case is the typical square one made of leaf fragments.

***Lepidostoma carrolli* Flint**

Lepidostoma carrolli Flint, 1958, pp. 22, 24, fig. 4.

An additional collection of two males of this species, one of which bears large setal patches on the terminal segments, shows that the species must be placed in the *vernalis* group.

Male (Fig. 8). Length of fore wing 5-7 mm. Maxillary palpi consisting of a single segment, flattened and curved dorsad as in *vernalis*. Readily distinguished from the other species by the structure of the tenth segment.

Ninth segment somewhat broader dorsally, the dorsal warts of moderate size. Clasper rather short and deep in lateral view, terminating in a blunt, bifid lobe; dorsal process fairly long, a quadrate, dentate plate extending vertically from its base. Aedeagus with an ovoid sclerite. Tenth segment variable, but consisting essentially of a pair of sclerotized, roof-like lobes overhanging the aedeagus; in a paratype from Lakehurst, N.J., the lobes are short and rounded (Fig. 8d), while in a specimen from Deer Isle, Maine (Fig. 8b), the lobes are produced into long apical points. Variation in the shape of the tenth segment was noted and illustrated in the original specimens of this species all of which were from Lakehurst, N.J., (Flint, 1958).

Female (Fig. 15). Similar in general structure to the male. Distinguished from females of the other species by the bilobed internal plate of the genitalia which extends slightly beyond the apex of the subgenital plate.

Ninth tergite rounded apically; tenth tergite with a small transverse carina. A bilobed internal plate extending slightly beyond apex of subgenital plate. A pair of small dark sclerites between this internal plate and the subgenital plate. Subgenital plate mostly membranous, margins indistinct. Ventral bridge of spermatheca bent at nearly 90 degrees at midline.

Material Examined. *Maine.* Sunset, Deer Isle: 1 ♂, VIII-20-59; 1 ♂, VIII-26-59.

Range and Habits. Previously known only from New Jersey, the species is now recorded from Maine. Flight of the adults is apparently restricted to the fall.

Nothing is known concerning the immature stages.

Latipennis Group

Lepidostoma latipennis (Banks)

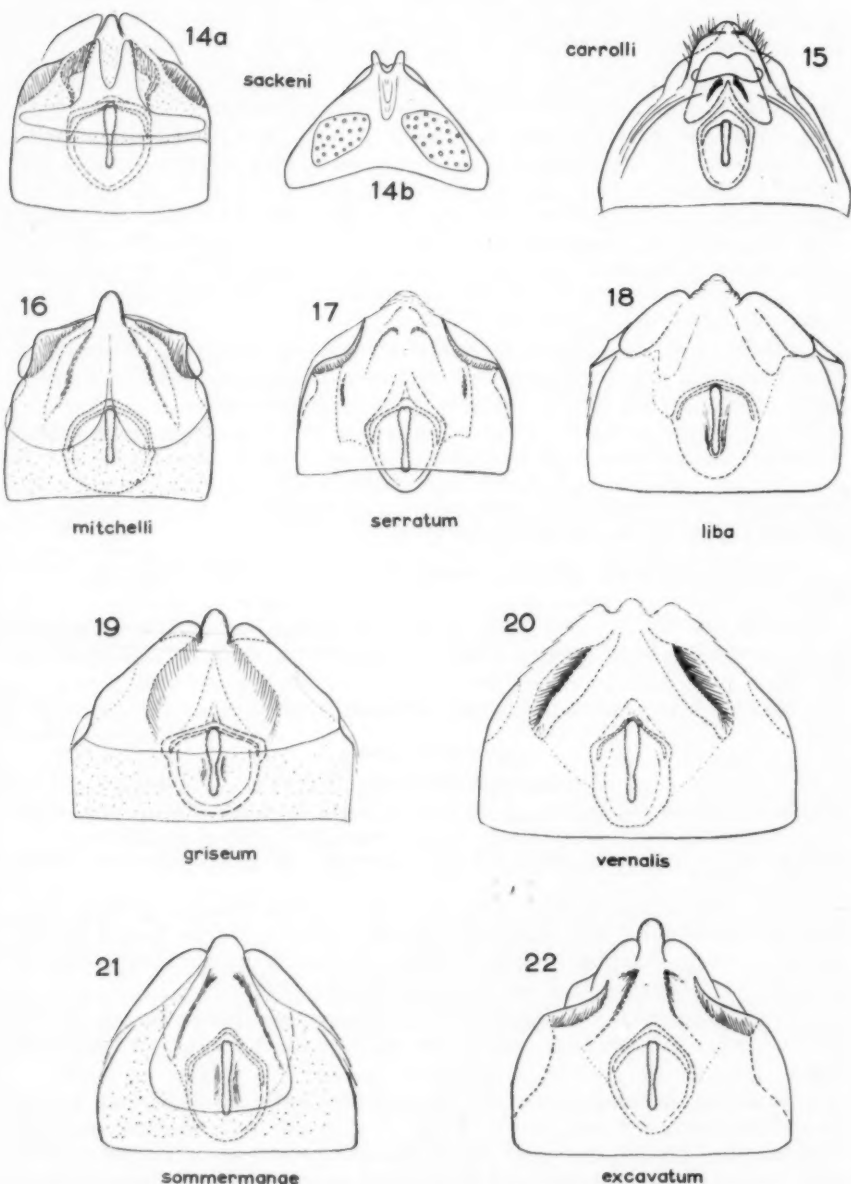
Notiopsyche latipennis Banks, 1905a, p. 216; Banks, 1905b, p. 11, pl. 2, figs. 20, 27; Ulmer, 1907, pl. 13, fig. 114; Carpenter, 1933, p. 35, fig. 14; Betten, 1934, p. 444, pl. 65, fig. 9.

Lepidostoma latipennis Ross, 1946, p. 272, fig. 3; Denning, 1949, p. 121; Morse and Bickler, 1953, p. 101.

This rather unique group consists of only the single species *latipennis*. The male has been figured and described a number of times, but the female has not been previously described. Certain unique characters in the female help to confirm the recognition of a distinct group for this species.

Female (Fig. 11). Distinguished from the females of other species by the external, lateral sclerotized pockets of the eighth segment, and by the sculptured bursa.

Similar in size to the male, but the maxillary palpi five-segmented and of normal structure, and not greatly thickened as in the male; scape of antennae very long and slender, somewhat longer than that of the male, but not as thick and without the thick cluster of mesal hairs occurring in the male. Wings somewhat narrower than in the male, and more acute apically. Genitalia chiefly characterized externally by a deep invaginated, sclerotized, lateral pocket at each side of the subgenital plate; internally, the most conspicuous feature is an elongate bursa with the end funnel-shaped and sculptured with rows of more-or-less octagonal sclerotized ridges; spermatheca broadly rounded, lateral bands heavily sclerotized, ventral bridge thin.



Figs. 14-22. Genitalia and terminal abdominal segments of *Lepidostoma* spp. females. 14, *L. sackeni*, 14a ventral view, 14b dorsal view; 15, *L. carrolli*, ventral view; 16, *L. mitchelli*, ventral view; 17, *L. serratum*, ventral view; 18, *L. liba*, ventral view; 19, *L. griseum*, ventral view; 20, *L. vernalis*, ventral view; 21, *L. sommermanae*, ventral view; 22, *L. excavatum*, ventral view.

Material Examined. *North Carolina.* Crabtree Meadows Camp Ground, Blue Ridge Parkway: 1 ♂, IX-16-58; many ♂, IX-2-59. Cashiers, Green Creek: 3 ♂ 2 ♀, IX-11-58. *South Carolina.* Walhalla Federal Fish Hatchery: 1 ♂ 1 ♀, IX-11-58.

Range and Habits. This species has previously been recorded from Georgia, North Carolina, New Hampshire and Nova Scotia. South Carolina is here added.

Adults of this species were emerging in numbers along the river at Crabtree Falls, N.C., in September, 1959. Careful searching under rocks and on pieces of submerged wood yielded several pupal cases, from which adults emerged a few days later. The larval sclerites were the uniform brown colour of most *Lepidostoma* larvae, while the cases were constructed of quadrate pieces of bark fastened together in the typical four-sided arrangement.

Unicolor Group

***Lepidostoma americanum* (Banks)**

Olemira americana Banks, 1897, p. 29; Ulmer, 1907, pl. 15, fig. 131; Banks, 1914, p. 265.

Olemira costalis Betten (*nec* Banks), 1934, pp. 405, 606, pl. 63, fig. 4, pl. 64, figs. 1-5.

Lepidostoma americanum Ross, 1946, pp. 284-85, fig. 14a; Morse and Blickle, 1953, p. 101.

The male of this species was figured by both Betten (as *costalis*) and Ross, but the female has not been described. Both the male and female genitalia show this species to be closely related to *costalis* (Banks).

Female (Fig. 13). Distinguished by the stronger development of the central sclerotized point on the ninth tergite and by the shape of the internal sclerites of the ninth and tenth segments.

Ninth tergite massive, almost concealing the tenth tergite, and developed into a central sclerotized point. Tenth tergite projecting as two small, rounded, membranous flaps. Ninth and tenth segments internally with a complex of sclerites. Spermatheca with no striking modifications; a slight projection where the ventral bridge is attached.

Material Examined. *North Carolina.* Highlands Biological Station, Highlands: 1 ♂ 5 ♀, VI-29 to VII-3-58. *Virginia.* Cave Mountain Lake, near Natural Bridge: 1 ♂, VII-8-58.

Range and Habits. The species has been recorded from Georgia, Massachusetts, New York, New Hampshire, and Virginia, and now North Carolina. The record for Manitoba, which Ross (1946) credited to Banks, is in error. Banks recorded the species only from Massachusetts and Virginia.

Adults were taken at lights in Highlands in early summer only, although collecting continued throughout the summer. Banks collected the type series in July, while Betten records August for his specimens.

Nothing is known of the immature stages.

***Lepidostoma frosti* (Milne)**

Atomyia frosti Milne, 1936, p. 119.

Lepidostoma frosti Ross, 1946, p. 279, fig. 8; Denning, 1949, p. 120; Morse and Blickle, 1953, p. 101; Denning, 1954, p. 193.

The male genitalia of this species have been figured by Ross, but the female has not been described previously. The genitalia of the female are typical of the species in the *unicolor* group, and seem closest to *unicolor* (Banks).

Female (Fig. 12). Distinguished from *unicolor* by the short ventral rod of the tenth tergite and by the lateral expansion of the ventral bridge of the spermatheca.

Dorsum of the ninth segment narrow, bearing an emarginate projection on its posterior margin. Tenth tergite bilobed, apices rounded; a slender sclerotized rod ventrally. Ventral bridge of spermatheca flaring slightly laterally.

Material Examined. *Massachusetts.* Williamsburg: cases with larval sclerites, VII-6-57. *New Hampshire.* Cutler River, Pinkham Notch: ♂ and ♀ pupae, VIII-4-58; larvae, VI-12-57. East branch Saco River, Dundee: larvae and pupae, VI-9-57. Ammonoosuc R., Zealand Camp Ground: larvae, VI-11-57. *North Carolina.* Camp Alice, Mount Mitchell: cases with larval sclerites, IX-1-59. *Tennessee.* Indian Gap, Great Smoky Mountains National Park: 1 ♂, VII-1-58.

Range and Habits. The species was previously known from Maine, Massachusetts, New Hampshire, Nova Scotia, and Quebec. Discovery of the species in North Carolina and Tennessee extends its range greatly.

Records indicate that the flight period of the adults is largely confined to July and August. Morse and Blickle recorded the adults from July 20 to 26 in the White Mountains of New Hampshire.

Of all the species of *Lepidostoma* in eastern North America that have been reared, the larva and case of this species are the only ones as yet readily recognizable. The cases are composed of small plant fragments placed transversely to form an irregular log-cabin type of structure. The sclerites of the larvae are yellowish, with brown spots. There are also western species which share these characteristics.

The larvae live in small, cold, tumbling mountain brooks from one to three yards wide. The pupal cases are attached to the undersides of rocks in the stream.

Summary

In a revision of the *vernalis* group of the genus *Lepidostoma*, four new species are added from the southern Appalachian region of eastern North America. The recently described *Lepidostoma carrolli* Flint is transferred to the *vernalis* group, making a total of ten species. Keys are provided for the males and females. In the *latipennis* group the female of *L. latipennis* (Banks) is described. In the *unicolor* group the females of *L. americanum* (Banks) and *L. frosti* (Milne) are described. The known distribution of each species treated is summarized, new records are added, and various observations on the habitat and general life history are offered.

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The Introduced Parasites of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae), with a Critical Evaluation of Their Usefulness as Control Agents

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Two aspects of the biological control of *R. buoliana* are reported in this paper. From 1949 to 1957 rearing techniques were developed for and observations were made of the abundance and biology of parasites received in host material that was collected in Europe (Arthur). From 1955 to 1959 a critical evaluation of the parasites was made, largely based on a study at Elmira, Ontario, of the biology and habits of five representative parasitic species in the field and the laboratory to determine factors that limit their efficiency (Juillet).

The European pine shoot moth, *Rhyacionia buoliana* (Schiff.), has been an important pest of pines in Europe for several centuries. Since it was first recorded in North America in 1914 (Busck, 1914), it has been accidentally reintroduced many times on nursery stock from Europe and now occurs from Massachusetts west to Illinois, and from West Virginia north to Ontario where it was first recorded in nursery stock imported from Holland (McLaine, 1926). Since that time it was reported from British Columbia (Mathers and Olds, 1940), the Maritimes (Reeks *et al.*, 1951), Newfoundland (Reeks *et al.*, 1954), and Quebec (Martineau and Béique, 1954) where it is largely confined to ornamental plantings. At present the main centers of infestation in large pine plantations

are in New York and Michigan in the United States, and southern Ontario in Canada.

R. buoliana has been recorded from many pine species (Butovitsch, 1936) but the most important hosts in eastern North America are: red pine, *Pinus resinosa* Ait.; dwarfed mountain pine, *P. mugo* Turra; Scots pine, *P. sylvestris* L.; and Austrian pine, *P. nigra* Arnold. In western North America *R. buoliana* could become an important pest on ponderosa pine, *P. ponderosa* Laws. (Friend and Hicock, 1935), and lodgepole pine, *P. contorta* Dougl. (Mathers and Olds, 1940).

The results of a study of the indigenous parasites that attack *R. buoliana* in Ontario and of their abundance showed few promising species (Watson and Arthur, 1959). Biological control attempts were initiated in Canada in 1928, and from then until 1959 twelve parasite species from Europe, totalling 86,000 individuals, were released in southern Ontario. In the United States over 300,000 individuals, of 15 species, were liberated in Connecticut, Massachusetts, New Jersey, New York, and Pennsylvania from 1931 to 1938¹. In both countries four species became established initially: *Orgilus obscurator* (Nees), *Temelucha interruptor* (Grav.), *Tetrastichus turionum* (Htg.), and *Pimpla turionellae* (L.) but only the first of these became common.

Material and Methods

From 1955 to 1959 a total of about 283,000 pine shoots infested with *R. buoliana* were collected in Europe and shipped by air express to the Entomology Research Institute for Biological Control, Belleville, Ontario. These shoots were collected in Austria, Belgium, England, Finland, Germany, and Sweden between early May and mid-July. They were incubated soon after arrival and a total of 38,000 individuals of 11 parasitic species were released at Elmira, Ontario.

Though many methods of handling the European material were used, the following was the most efficient. The shoots were cut from the trees and dropped into metal tins lined with paper to absorb the moisture, as described by Maw (Coppel *et al.*, 1955). The tins were kept in a cool place for three days and the excess moisture was removed daily. Then the tins were lined with many layers of absorbent paper, tightly sealed with gummed paper, and shipped by air express, part of the trip being completed by rail at night. Upon arrival at Belleville the shipments were kept at 44°F. until they were incubated. The infested shoots from each country were incubated separately at about 72°F. and 60 per cent relative humidity.

When large amounts of material were received, the shoots were placed in shallow, screened-bottom trays (Arthur *et al.*, 1958). The trays were stacked and the insects escaped through the space left by the low sides. The parasites were collected individually in glass vials on a bleached cotton sheet fastened over the window. When small numbers of shoots were received, they were placed in cardboard or screened-bottom wooden boxes as described by Arthur (Arthur and Juillet, 1957). The boxes were half filled with shoots and the insects escaped into vials placed over two holes near the top of each box. The sex and specific determination of each parasite were made with the aid of a binocular microscope.

The daily emergence was recorded and the parasites were held in screened cages and fed on an aqueous solution of honey. The parasites mated in the cages,

¹P. B. Dowden, Northeastern Forest Experiment Station, 335 Prospect St., New Haven, Conn., U.S.A., in personal communication.

and when a sufficient number of one species had been accumulated they were shipped by rail, at night whenever possible, to the field for release.

The release techniques were improved considerably by liberating the parasites in the evening when the temperature and light intensity were decreasing thus minimizing their activity. When the weather forecast for the following days was unfavourable, such as low temperature, high wind, or rain, the releases were delayed until a clear warm day with little or no wind was expected. Mated females were released to increase the chances of initial establishment.

The methods used to study the biology and habits of five species of parasites were described recently (Juillet, 1959, 1960a, 1960b).

Results

Egg Parasites

No egg collections of *R. buoliana* were included in the shipments from Europe. *Copidosoma geniculatum* (Dalm.) was formerly considered to be an important egg parasite of *R. buoliana* (Ruschka, 1924) but it is now known to be a parasite of *Exoteleia dodecella* (L.) which also infests pine shoots and not of *R. buoliana*. The similarity of the host larvae, both in colour and feeding habits, led to the former error. The differences between the larvae of these species and the damage they cause are adequately described by Martin (1959). From collections of 300 larvae of the two species made at Newcastle, Ontario in 1957, at a time when the larvae of these two species were easily separated by size, 3.6 per cent of the larvae of *E. dodecella* and none of *R. buoliana* were found to be parasitized by *C. geniculatum* (Arthur *et al.*, 1958). Similar collections of the two species from Brighton, Ontario, in 1960, showed that 7.5 per cent of the larvae of *E. dodecella* and none of the *R. buoliana* were parasitized by *C. geniculatum*. Releases of this species in Canada were made at Niagara Falls, Ontario in 1936 and at Elmira, Ontario from 1955 to 1957. It was recovered, presumably on *E. dodecella*, at the former location in 1941 and at the latter in 1956. Martin (1959) also recorded the species as being established on *E. dodecella* at Vernon and Winchester, Ontario.

In Europe *Trichogramma evanescens* Westw. was reported as an egg parasite of *R. buoliana* (Thorpe, 1930) and the species was imported into the United States in 1936 and 1937, when 115,000 individuals were released against *R. buoliana* in Connecticut and New Jersey. No recoveries have been reported. Friend and West (1933) recorded the native *T. minutum* Riley as a parasite of *R. buoliana* in Connecticut. The present authors recorded it from Brighton (1954) and Elmira (1956, 1957) in insignificant numbers. It is doubtful that these egg parasites will ever become important enemies of *R. buoliana*. The females of *R. buoliana* deposit their eggs singly and sporadically over large areas of foliage. Thus, even in high infestations, the female parasites would have to search for each egg separately and, as these *Trichogramma* females attack practically any lepidopterous eggs, they would scatter their progeny among the first hosts encountered and so be less effective against *R. buoliana*.

Internal Larval Parasites

Surveys of the native parasites of *R. buoliana* in Ontario (Watson and Arthur, 1959) revealed that no parasites belonging to this group were common. In Europe there are seven common internal larval parasites (Table I). One species, *Actia nudibasis* (Stein.), attacks the late instar larvae and the progeny emerge about two months later to attack some other species of hosts. The other six species attack the needle-mining larvae; their progeny overwinter as young

larvae within the hibernating host and emerge as adults in time to attack the larvae of the next generation. These species except for most of the *Eulimneria rufifemur* (Thoms.) from Continental Europe emerge from the European collections in time to be released against North American infestations during the same year. These latter species are susceptible to the same mortality caused by low winter temperatures as is their host, which was reported to be 50 per cent at -18°C . in Germany (Berger and Cramer, 1957) and 100 per cent at -28°C . in North America (West, 1936). In England Harris (in press) found no significant winter mortality.

Orgilus obscurator (Nees).—This braconid was the most abundant and most widely distributed parasite of *R. buoliana* obtained from the European collections (Table I). Thorpe (1930) stated that it is widely distributed throughout Europe, as far south as Italy and Corsica. The adults started emerging shortly before the peak emergence of the host and thus were available during the period of greatest vulnerability of the host. Both sexes occurred in about equal numbers. A high fecundity and a high efficiency in finding its host (Juillet, 1960a) make it a valuable parasite. In over 2,000 host larvae dissected, never more than one *O. obscurator* larva was found per host but in all instances of multiparasitism, *O. obscurator* was invariably suppressed. Experiments show that it is as resistant to low temperatures as its host and that there is no difference in mortality between parasitized and unparasitized hosts (Juillet, 1960b). The species has a slow dispersal rate which, according to Sellers (1953), results in an equilibrium of distribution and an effective control more quickly, but in a proportionately smaller area, than species with fast dispersal rates. However, as the males disperse twice as fast as the females (Juillet, 1960a), the equilibrium of distribution mentioned by Sellers may not be produced.

This species was first recorded in the United States in 1925 (Dowden and Berry, 1938) but, as it was not released until 1931, its presence must have resulted from an earlier accidental introduction within infested nursery stock. Prior to 1934 *O. obscurator* had been recorded from 23 localities in southern Ontario though it had been released at only five. This indicates that much of its early dispersal resulted from shipments of infested European stock or from stock originating in infested Canadian nurseries. *O. obscurator* was recovered from Easton, Connecticut (Dowden and Berry, 1938) where only 54 females had been released. These data imply that relatively small numbers are required to establish the species in a new area. After the severe winter of 1933-34, when the host was virtually eliminated, the species was recovered in only seven urban localities in Ontario. More recently it was recorded from eight out of fifteen rural localities surveyed (Watson and Arthur, 1959). In the United States it is now common in the northeastern states and is present in Michigan (Miller, 1960) where it has not been released.

Records show that, in the United States, 14 releases were made in four states, Connecticut, Massachusetts, New York and New Jersey, with an average of 130 females per release; and prior to 1955 in Canada 14 releases were made with an average of 220 females per release. From 1955 to 1959 concentrated releases were made at Elmira, Ontario, with an average of 900 females per release. There are no records of the proportion of parasites released to host present at the time of the initial liberations but at Elmira it was estimated that for every female parasite released there were 10,000 host larvae. Even with these overwhelming odds in favour of the host, parasitism increased from 0.1 per cent in 1955 to 14.1 per cent in 1959. During this period the winter mortality of the host

TABLE I
Species and relative abundance of common parasites of *R. buoliana* obtained from Europe between 1954 and 1958

| | England, 1954-1958 No. hosts collected 62,849 | | Belgium, 1955-1957 No. hosts collected 60,600 | | Germany, 1957 No. hosts collected 28,050 | | Austria, 1955 and 1957 No. hosts collected 66,370 | | Sweden, 1957-1958 No. hosts collected 9,368 | | Finland, 1957 No. hosts collected 4,820 | | Average | |
|--|--|--|--|--|---|----------------------------|--|--|--|----------------------------|--|----------------------------|---|----------------------------|
| | Per- cent in order para- sitism | Range in order of abun- dance | Per- cent in order para- sitism | Range in order of abun- dance | Per- cent in order para- sitism | Order of abun- dance | Per- cent in order para- sitism | Range in order of abun- dance | Per- cent in order para- sitism | Order of abun- dance | Per- cent in order para- sitism | Order of abun- dance | Per- cent in order para- sitism | Order of abun- dance |
| A. Internal larval parasites | | | | | | | | | | | | | | |
| <i>Ogilus obscurator</i> (Nees) | 8.9 | 1-3 | 2.4 | 1-3 | 3.1 | 3 | 3.8 | 1 | 12.1 | 1 | 0.1 | 1 | 5.0 | 1 |
| <i>Temelucha interruptor</i> (Grav.) | 5.8 | 2-3 | 1.7 | 3-4 | 4.1 | 1 | 2.0 | 2 | 0.4 | 6-7 | 0.1 | 2 | 3.1 | 2 |
| <i>Eulimneria rufifemur</i> (Thoms.) | 1.5 | 2-6 | 3.0 | 1-2 | 0.9 | 4 | <0.1 | 11 | 0.2 | 8 | Unrecorded | 3 | 1.3 | 4 |
| <i>Actia nudibasis</i> Stein. | 0.4 | 5-7 | 0.2 | 5-A | 0.1 | 7 | <0.1 | 13 | 1.5 | 2-4 | Unrecorded | 4 | 0.2 | 9 |
| <i>Pristomerus</i> sp. | Absent ¹ | | 0.3 | 6 | 0.7 | 5 | <0.1 | 14 | 0.3 | 7-U ^a | Unrecorded | 8 | 0.2 | 8 |
| <i>Eulimneria mutabilis</i> (Holmg.) | 0.1 | 6-A ¹ | 0.4 | 5-A | 0.3 | 8 | 0.1 | 8 | Unrecorded | 9 | Unrecorded | 11 | 0.2 | 11 |
| <i>Omorgus borealis</i> (Zett.) | Absent | | Absent | | Absent | | Absent | | 0.1 | | Unrecorded | 14 | <0.1 | 14 |
| B. External larval parasites | | | | | | | | | | | | | | |
| <i>Epiphialtes ruficollis</i> (Grav.) | 7.7 | 1-4 | 0.1 | 8-A | <0.1 | 13 | 0.3 | 6 | 0.1 | 3-9 | Unrecorded | 3 | 2.2 | 3 |
| <i>Exeristes rubrorator</i> (F.) | Absent | | <0.1 | 11-A | <0.1 | 11 | 1.3 | 3 | Unrecorded | | Unrecorded | 6 | 0.5 | 6 |
| <i>Scambus sagax</i> (Htg.) | 0.8 | 4-9 | <0.1 | 8-9 | 0.1 | 6 | 0.1 | 10 | 1.2 | 3-U | <0.1 | 3-U | 0.3 | 7 |
| <i>Bracon brevicornis</i> (Wesm.) | Absent | | Absent | | 0.1 | 9 | 0.3 | 5 | Unrecorded | | Unrecorded | 10 | 0.2 | 10 |
| <i>Scambus buolianae</i> (Htg.) | 0.1 | 8-A | <0.1 | 11-A | <0.1 | 12 | 0.1 | 7 | 0.5 | 4 | <0.1 | 3-U | 0.1 | 13 |
| <i>Scambus brevicornis</i> (Grav.) | Absent | | Absent | | <0.1 | 14 | <0.1 | 12 | Unrecorded | | Unrecorded | 15 | <0.1 | 15 |
| <i>Bracon</i> spp. | <0.1 | 7-A | <0.1 | 10-A | Absent | | Absent | | Unrecorded | | Unrecorded | 16 | <0.1 | 16 |
| C. Pupal parasites | | | | | | | | | | | | | | |
| <i>Tetrastichus turionum</i> (Htg.) | Absent | | 0.1 | 6-10 | 1.1 | 4 | 0.9 | 4 | <0.1 | 10-U | Unrecorded | 5 | 0.6 | 5 |
| <i>Pimpla turionellae</i> (L.) | 0.3 | 5-9 | <0.1 | 9-A | 0.1 | 10 | 0.1 | 9 | 0.7 | 2-4 | Unrecorded | 12 | 0.1 | 12 |
| D. Hyperparasite | | | | | | | | | | | | | | |
| <i>Perilampus tristis</i> Mayr. ² | Absent | | 3.2 | | 2.1 | | 0.2 | | Unrecorded | | Unrecorded | | 1.6 | |

¹A or Absent = no parasites of this species obtained though a large sample, at least 20,000 infested buds, had been incubated.

²U or Unrecorded = no parasites of this species obtained but sample incubated too small to determine absence from complex.

³Parasitism of *P. tristis* was calculated on the basis of the number of *R. buoliana* collected so that its abundance could be directly compared.

averaged about 50 per cent and was much lower below the snowline (maximum 10 per cent) than above. As *O. obscurator* prefers to attack the host on the lower half of the trees, its chances of survival is greatly increased.

Temelucha interruptor (Grav.).—This ichneumonid was obtained from all European localities where collections were made and, except from Sweden, was the second most abundant parasite of *R. buoliana* (Table I). *T. interruptor* emergence began when host emergence was at its peak and reached its peak about a week later. The ratio of females to males was 3:2.

T. interruptor has a high fecundity but is inefficient in finding its host (Juillet, 1960a). The species was observed to lay up to 80 per cent of its eggs (representing 0.9 per cent of the *O. obscurator* population) in larvae already parasitized by *O. obscurator* and to survive over the latter species. This high frequency of multiparasitism by *T. interruptor* may be detrimental to effective control and reduces its value as a control agent if its population increases. Tests revealed that the species is slightly less resistant to low temperatures than is its host. Also it appears to prefer to attack the upper half of the infested trees where mortality from low winter temperatures is more apt to occur. The rate of dispersal of both sexes is similar to that of the males of *O. obscurator*.

A total of 22 releases of *T. interruptor* were made in Connecticut, Massachusetts, New York, and New Jersey in the United States, from 1931 to 1937 with an average of 500 females per release. Although larger releases were made of *T. interruptor* than of *O. obscurator*, they were recovered in only three localities as compared to nine for *O. obscurator* (Dowden and Berry, 1938).

A total of 16 releases were made in Ontario prior to 1955, with an average of 1,100 females per release. *T. interruptor* was recovered at three urban release points in the Niagara Peninsula. It parasitized approximately five per cent of the *R. buoliana* larvae at two of these locations (Coppel and Arthur, 1954). Subsequent surveys at 15 widely dispersed localities indicate that this species, unlike *O. obscurator*, has failed to disperse to rural plantations (Watson and Arthur, 1959). From 1955 to 1959 concentrated releases at Elmira, Ontario, were made at the rate of 1000 females per release or approximately one female for every 9,000 host larvae available for parasitism. Ninety-two per cent of the Ontario releases were in synchronization with the host. At Elmira where *T. interruptor* and *O. obscurator* were released under the same conditions, *T. interruptor* increased from zero parasitism in 1955 to 0.5 per cent in 1959.

Eulimneria rufifemur (Thoms.).—This ichneumonid was the fifth most abundant parasite of *R. buoliana* obtained from the European collections (Table I). It was present in all countries where collections were made except Finland, where the collections were actually too small to represent the parasite complex.

E. rufifemur emerges over a two to three month period. Adult parasites emerged early in material from England and in synchronization with the susceptible stage of *R. buoliana* in North America but late in material from Continental Europe and out of synchronization with the host in North America (Table II). Thus, while the species is relatively abundant in Belgium, it emerges too late to be released the same year against *R. buoliana*. The sharp difference in the period of adult emergence between England and Continental Europe indicates that two races might occur. Those individuals emerging too late for release can be reared in the laboratory on young larvae of *Anagasta kübniella* (Zeller) or *Plodia interpunctella* (Hbn.). On these hosts *E. rufifemur* completes its larval development without diapause and overwinters within its cocoon. Both sexes

TABLE II

Percentages of *Eulimneria rufifemur* adults which emerged from European collections in relation to the period when the susceptible stage of *R. buoliana* was available in Canada

| Periods | England | Belgium | Germany | Canada |
|--------------|---------|---------|---------|--------|
| May II | 0 | 0 | 0 | 0 |
| June I | 45.2 | 0 | 5.8 | 0 |
| June II | 49.3 | 0 | 2.9 | 5 |
| July I | 2.7 | 17.0 | 3.8 | 45 |
| July II | 2.7 | 16.0 | 3.8 | 45 |
| August I | 0 | 46.0 | 42.1 | 5 |
| August II | 0 | 21.0 | 41.6 | 0 |
| % parasitism | 1.5 | 3.0 | 0.9 | |

occurred in equal numbers on *R. buoliana* but the ratio of females to males was 2:1 on *A. kübniella* and *P. interpunctella*.

E. rufifemur has a relatively low fecundity but is fairly efficient in finding its host (Juillet, 1959). However, it is unable to detect parasitized from unparasitized larvae. This inability to prevent multiparasitism is prejudicial and lessens the value of the species as a control agent. A few larvae tested for tolerance to low temperatures appeared to be as susceptible to cold as *T. interruptor* and, as the species prefers the upper half of infested trees for oviposition, it cannot become important where winter mortality of the host is high. *E. rufifemur* has approximately the same rate of dispersal as *O. obscurator* (males twice as fast as females) and theoretically, unless immigrants replace the emigrants, the species is unable to produce an equilibrium of distribution in our North American conditions where releases are made at a few locations with relatively small infestations scattered over wide areas. Brooks and Brown (1936) stated that the species breeds much better than *T. interruptor* in uneven-aged stands, the condition being reversed in even-aged stands. The present authors feel that the previous statement would be true only in mixed stands.

There was one release of 10 females at Buffalo, New York, in 1935. There were two releases of 468 and 13 females at Niagara Falls and Toronto respectively in 1935, and four releases averaging 160 females each at Elmira between 1955 and 1958 where only 40 per cent of the females were liberated in synchronization with the susceptible stage of the host. At Elmira these releases represent approximately one female for every 100,000 host larvae, so it is not surprising that the species has not been recovered to date.

Actia nudibasis Stein.—This tachinid was obtained from all European countries except Finland where collections were made (Table I). It was the second most abundant parasite of *R. buoliana* in Sweden. It is probable that it was more abundant than is indicated in Table I, as the incubation method used was adjusted to secure the more numerous hymenopterous species. That this method was unsuitable for Diptera is indicated by the fact that over 60 per cent of the dipterous parasites received in 1955 died in their puparia before emerging. Both sexes occurred in approximately equal numbers.

Thorpe (1930) stated that *A. nudibasis* has probably often been confused with the closely related *A. pilipennis* (Fall.) which also attacks *R. buoliana* in Europe. It is likely that the two species have similar life histories and hosts. Escherich (1931) reported that *A. pilipennis* and *A. crassicornis* (Mg.) have two generations a year, the winter generation in *Evetria resinella* (L.) and the summer

generation in *R. buoliana*. This information would indicate that *A. nudibasis* also requires an alternate host.

Records show that three releases were made in Connecticut and Massachusetts in the United States from 1932 to 1935 averaging about 100 females per release. Four releases were made at Elmira, Ontario from 1955 to 1958, averaging 40 females per release, of which only 20 per cent were released in synchronization with the host. No recoveries were reported.

Pristomerus sp. probably *vulnerator* (Panz.).—This ichneumonid was not reared in material from England and Finland but was present in that from the other countries (Table I). The adults began to emerge when the host emergence was at its peak and continued for about a month. Thus emergence is synchronized with the host. The ratio of females to males was 2:1.

Ratzeburg (1840) listed *P. vulnerator* as among the four most important parasites of *R. buoliana* in Europe. Rosenberg (1934) recorded it as a parasite of *Carpocapsa pomonella* L. in France where it emerged at about the same time and over the same period as from *R. buoliana*. He also mentioned its recorded occurrence in England though Thorpe (1930) did not include it in his list of *R. buoliana* parasites. As this species was recorded from a large number of hosts in a variety of habitats (Rosenberg, 1934), it would probably be ineffective against a heavy infestation of *R. buoliana*.

One release of 30 females was made in Connecticut in 1937 and one of 13 and one of 70 females were made at Elmira in 1955 and 1957 with 13 and 51 of these released when the susceptible stage of the host was available. No recoveries were made.

Eulimneria mutabilis (Holmg.).—This ichneumonid was obtained from all countries except Sweden and Finland (Table I). It ranked ninth in abundance. Adult emergence occurred in two peaks, one before host emergence and the other after it. The species is thus poorly synchronized with its host. The ratio of females to males was 2:1.

Thorpe (1930) recorded it from 12 lepidopterous hosts from a variety of habitats. Brooks and Brown (1936) stated that it has two generations a year: the first on *R. buoliana* from which it emerges in early spring, the second on the winter moth, *Operophtera brumata* L. It emerges from the latter host in mid-summer to reattack *R. buoliana*.

In the United States there were two releases of 12 and 47 females in Connecticut and New York in 1937 and five releases, averaging 280 females per release, in Ontario from 1928 to 1943. All Canadian releases were synchronized with the host. One specimen was recovered (Coppel and Arthur, 1954) in Ontario in 1943.

Omorgus borealis (Zett.).—A small number of this ichneumonid was obtained from Sweden only (Table I), though Thorpe (1930) recorded it from *R. buoliana* in England and stated that it is known throughout north and central Europe. The same author reported it from nine other lepidopterous hosts.

One release of 55 females was made in Connecticut in 1937 but no recoveries were reported.

Considering the internal larval parasites as a whole, *O. obscurator* is the most valuable species. It has a high fecundity combined with efficient host-finding capabilities. It is as cold-hardy as its host and prefers to attack those hosts on the lower part of the tree that are most often below the snow-line. *T. interruptor* is a less valuable species because it competes directly with *O. obscurator* and is the survivor when both species occur in the same host larva.

However, it could be introduced into areas where winter mortality of the host is low and where *O. obscurator* has failed to become established. *E. rufifemur* should be considered for introduction only into areas where uneven-aged, mixed stands occur. *A. nudibasis* and *Pristomerus* sp. may be useful species and deserve further study.

External Larval Parasites

Studies on the indigenous parasite complex of *R. buoliana* in North America showed that four common external larval parasites account for three to six per cent parasitism (Watson and Arthur, 1959). As three of these species attack the late-instar *R. buoliana* larvae which are present from mid-May to mid-June they require an alternate host later in the summer. It is suspected that it is the lack of an abundant supply of alternate hosts that prevents these native species from becoming more efficient parasites. From the European collections there were seven common species of external larval parasites (five ichneumonids and two braconids), all of which require alternate hosts. These parasites attack the late-instar of *R. buoliana* and emerge during July or August to attack the larvae of other hosts.

The members of this group are unable to distinguish unparasitized larvae from those already parasitized by internal larval parasites and oviposit freely on both. This secondary parasitic role, though apparently accidental, results in the death of the internal parasites. The adults of these species feed on host body fluid and this predacious habit causes the death of additional *R. buoliana* larvae. Thus the importance of this group is greater than is indicated by percentage parasitism alone.

The parasites obtained from the European collections emerge too late to be released against *R. buoliana* during the same year. However, most previous releases were made the year the parasites were received and the parasites were thus out of synchronization with the host. Unless adequate numbers of a possible alternate host are present in or near the *R. buoliana* infestation, it would be preferable to propagate such parasites in the laboratory and release the resulting stock early the following summer when the late-instar larvae of *R. buoliana* are present in the field. Most of these species can be reared easily on mature larvae of the greater wax moth, *Galleria mellonella* (L.), or on spun-up larvae of the red-headed pine sawfly, *Neodiprion lecontei* (Fitch), which have been removed from their cocoons. The wax moth larvae are coddled by immersion in hot water (53° C.) for just over one minute and placed in sections of pine shoots hollowed out by mechanical means. The eggs laid on these larvae are then removed and placed individually on coddled wax moth or sawfly larvae in gelatin capsules. Occasionally more than one host larva is required before feeding is complete.

Epibialtes ruficollis (Grav.).—This ichneumonid was much more abundant in England than in the other countries where collections were made (Table I). In the 1955 English collection it was four times as abundant as any other parasite. Thorpe (1930) reported that the male is unknown but in the present collections males were as abundant as females. The species has a relatively low fecundity (Juillet, 1959).

A total of 949 individuals of *E. ruficollis* were released in Connecticut and New York in 1935 and 1936, and 7,032 were released in Ontario from 1933 to 1943 (Coppel and Arthur, 1954). No recoveries were reported. At Elmira a total of 4,382 adults were liberated between 1955 and 1957, of which only three

per cent were synchronized with *R. buoliana*. The species was not recovered from a total of 8,900 infested shoots collected from the area.

Exeristes roborator (F.) and *Bracon brevicornis* Wesm.—Both these species were most abundant in Austria though present also in Germany (Table I); *E. roborator*, though not *B. brevicornis*, was also present in Belgium. However, two other *Bracon* species were obtained from the Belgian material. This is the first record of *B. brevicornis* as a parasite of *R. buoliana*, though both species have long been recognized as important parasites of the European corn borer, *Ostrinia nubilalis* (Hbn.). In areas where corn, *Zea mays* L., and pine grow together these parasites attack *R. buoliana* in early summer and *O. nubilalis* in late summer. On *R. buoliana* the ratio of females to males of *E. roborator* is 1:2 and of *B. brevicornis* 1:1.

Preliminary tests revealed that *E. roborator* survives temperatures of -4°F . but not -14°F . (Maw and Arthur, 1958).

Between 1922 and 1938 large numbers of *E. roborator* (314,766) and of *B. brevicornis* (2,820,403) were released in the United States against *O. nubilalis* throughout the area now infested by *R. buoliana*. These releases were made mostly before 1930 when *R. buoliana* was starting to become more widespread and abundant. Initial recoveries of *E. roborator* were made, but the species failed to become permanently established (Baker *et al.*, 1949) because of poor synchronization with alternate hosts in areas where the corn borer has only one generation a year (Baker and Jones, 1934). *B. brevicornis* was not recovered and no logical reason for its failure could be found (Baker *et al.*, 1949). In Ontario 217,643 *E. roborator* and 3,553,383 *B. brevicornis* were liberated against *O. nubilalis* between 1923 and 1933, but mostly before 1930 (Baird, 1938). They also failed to become permanently established after these releases. At Elmira where pine and corn are grown in adjacent fields, a total of 839 *E. roborator* were released in 1957 and 1958 of which about 70 per cent were in synchronization with *R. buoliana*. Initial establishment was recorded.

Scambus sagax (Htg.), *S. buolianae* (Htg.), and *S. brevicornis* (Grav.).—The first two species were obtained from all countries where collections were made and the third from Austria and Germany only (Table I) but none were abundant. The population of *S. sagax* from England has a tendency to go into diapause when the humidity during the incubation is low. Under moist conditions 19 per cent entered diapause and under dry conditions this increased to 74 per cent. Females predominated in all three species with ratios of 3:1, 2:1, and approximately 4:1 respectively.

Preliminary experiments showed that *S. buolianae* and *S. brevicornis* survive temperatures of -4°F . but not -14°F . (Maw and Arthur, 1958).

A total of 141 *S. sagax* and 785 *S. buolianae* were released in Ontario from 1955 to 1958 of which about 40 per cent were synchronized with *R. buoliana*. No recoveries have been made to date.

In general, the present authors feel that external larval parasites should not be released unless an abundant supply of known alternate hosts is present in the area. However, it is felt that the possibility of using *P. ruficollis* and *E. roborator* against *R. buoliana* in North America should be more thoroughly investigated.

Pupal Parasites

Surveys of the indigenous parasites attacking *R. buoliana* in Ontario showed that only one species commonly attacks the pupa (Watson and Arthur, 1959).

From the European collections two common species were obtained: *Tetrastichus turionum* (Htg.) and *Pimpla turionellae* (L.). The parasitism shown for these species in Table I is much lower than the true values since a large percentage of the European collections were made in the larval stage before the host was susceptible to attack by these pupal parasites.

Tetrastichus turionum (Htg.).—This chalcid was the fifth most abundant parasite of *R. buoliana* obtained from the European collections (Table I). It was especially important in Austria, Belgium, and Germany but was absent from England. This gregarious parasite, averaging 23 adults per pupa, has one generation a year and emerges in time to attack the next generation of *R. buoliana*. Observations on 94,000 infested shoots from Austria and Germany showed that about 11 per cent of the *T. turionum* emerged during the same year as collected while the remainder overwintered as mature larvae within the pupal cases of the host. Most of the *T. turionum* that emerged the same year were from shoots that had been infested by the previous generation of *R. buoliana*, the remainder were from the few *T. turionum* that did not go into diapause. The ratio of females to males was 7:1.

Under laboratory conditions *T. turionum* laid an average of 45 eggs per female (Juillet, 1959). Though these eggs were deposited on a small number of host pupae, both the favourable sex ratio and the fact that the sexes emerge together ensure a high population increase within a few generations. In addition they do not lay on host pupae that are already parasitized and do not lay more eggs than can reach maturity in any one host. Laboratory tests showed that 83 per cent of the overwintering larvae survived exposures to -23°C . for up to 13 hours, but only 65 per cent emerged as adults (Juillet *et al.*, 1958). In nature the parasitized host pupae within the shoots may remain on the trees until spring but most are blown to the ground where they obtain maximum snow protection during the winter.

A total of 196,525 adults of *T. turionum* were released at 12 localities in Connecticut, Massachusetts, New York, and New Jersey from 1933 to 1937, and 1,570 at Kingsville, Ontario, in 1938. Dowden and Berry (1938) reported recoveries from four areas in the United States and Coppel and Arthur (1954) from Kingsville where approximately five per cent of the *R. buoliana* pupal population was parasitized by this species. Subsequent surveys in Ontario showed that the species had not dispersed out of the Kingsville area (Watson and Arthur, 1959). In attempts to increase the distribution of this species 15,052 adults were liberated at Elmira and Clear Creek, Ontario, from 1956 to 1958 but no recoveries have been made to date.

Pimpla turionellae (L.).—This ichneumonid, formerly known as *Ephialtes examiner* F., was recorded from all areas where collections were made except Finland (Table I). The adults emerging from the European collections were too late for release against *R. buoliana* the same year. For synchronization with *R. buoliana*, they would have to be reared in the laboratory. This species has been reared on a variety of lepidopterous pupae, the most efficient for propagation being those of the greater wax moth, *G. mellonella*. Releases could be made in late summer if pupae of known alternate hosts were present in sufficient numbers in the vicinity of the *R. buoliana* infestation. Both sexes occurred in equal numbers on *R. buoliana*. However, laboratory studies indicate that a higher percentage of females emerge from larger hosts (Arthur and Wylie, 1959).

Berry (1939) reported an average progeny of 55 per female when reared on the ugly-nest caterpillar, *Archips cerasivoranus* (Fitch), but the number of host

pupae destroyed was greater due to the predatory habit of the adult parasites feeding on the host body fluid. The same author stated that 90 per cent of the overwintering adults survived temperatures of -11°F . Thorpe (1930) reported the species as attacking 39 lepidopterous hosts which occur in a variety of habitats. It attacks *R. buoliana* in early summer and one or more other hosts in late summer and autumn.

A total of 11,270 adults (mostly mated females) were released in Connecticut, New York, and New Jersey, from 1935 to 1938, but most of these were out of synchronization with *R. buoliana* (Berry, 1939) and no recoveries were reported. A total of 2,092 adults were released in Ontario from 1935 to 1937. Initial establishment was obtained at six localities (Coppel and Arthur, 1954). From 1952 to 1958 a total of 1,457 adults were liberated at Brighton and Elmira, Ontario. Initial establishment was reported at Brighton by Arthur (Coppel *et al.*, 1955).

T. turionum is the only pupal parasite recommended for release against *R. buoliana* in North America. It is cold-hardy and requires no alternate hosts. Because many individuals of both sexes emerge from one host, relatively few parasitized hosts would be required for establishment and the parasite should be able to maintain itself even when host populations are low. A number of scattered but sizeable releases (1,500 females) rather than one large release should be made as this species apparently has low powers of dispersal. *T. turionum* larvae remain within the parasitized *R. buoliana* pupae inside the infested shoots during the late summer months. In this position they would be exposed to accidental predation by the larvae of *Dioryctria abietivorella* (Grote) which often infest such shoots. It might be advisable not to release *T. turionum* in areas such as Elmira where *D. abietivorella* is abundant.

Hyperparasites

The most important hyperparasite reared from the European material was *Perilampus tristis* Mayr. This chalcid was absent from England and unrecorded from Sweden and Finland (Table I). It was the second most abundant parasite from Belgium and the fourth most abundant from Germany. The emergence of *P. tristis* began when the host emergence had reached its peak and continued for approximately one month.

This species causes heavy mortality to *R. buoliana* parasites in Europe (Bergold and Ripper, 1937). It is especially destructive against *E. ruficollis* and *P. turionellae* but those species such as *O. obscurator* and *T. interruptor*, which pupate early in the season, are more resistant to its attack.

It is of the utmost importance that *P. tristis* not be introduced into North America.

Discussion and Conclusions

Many of the parasites of *R. buoliana* that have already been introduced have appeared to be ineffective. The present authors feel that the conditions under which these releases were made were largely unfavourable to successful establishment or population build-up.

In Ontario during the early 1930's *R. buoliana* parasite releases were limited to ornamental plantings in urban areas such as parks and cemeteries. Such infestations were often scattered and of limited extent, usually less than half an acre. As labour was cheap during the depression, any infested shoots within reach were gathered and burned. Parasites released under such conditions stood a good chance of being destroyed even though they had succeeded in finding hosts which were scarce due to constant pruning².

²Report of the Dominion Parasite Laboratory, Belleville, Ontario, 1929-30 (Unpublished).

It is now known that many adult parasites prefer to feed on the flowers of Umbelliferae though they will feed sparingly in the laboratory on flowers of Leguminosae, Asclepiadaceae, Cruciferae, and Compositae (Leius, 1960). If released in urban areas where such plants are scarce or absent, adult parasites might leave in search of these flowers and never return to the *R. buoliana* infestation. Entomologists in the U.S.S.R. plant Umbelliferae in orchards so that parasites can feed on them (Simmonds, 1959).

The important internal larval parasites, *O. obscurator*, *T. interruptor*, and *E. rufifemur*, have dispersal rates much too great for the size of the areas where the early releases were made. Thus most of the parasite populations released in such small areas would become lost in the surrounding uninfested area and those remaining in the infested area would be prevented from increasing to economic levels.

All external larval parasites, except a small percentage of *S. sagax* from England and also the pupal parasite, *P. turionellae*, require alternate hosts. Such hosts would be in short supply in and around urban areas where attempts are frequently made to control all insect populations. Thus attempts to establish these species in such areas are unlikely to succeed.

In general *R. buoliana* in Europe occurs in areas which do not have the low winter temperatures experienced in Ontario and Michigan. Thus many of the parasites collected in the heavily infested areas of Europe may not be able to overwinter successfully in our climate. As the majority of the parasites released in Ontario during the 1930's were from England, where little or no winter mortality occurs, this may be one reason for the comparatively poor results obtained from these introductions.

In the United States many releases appeared to have been made in large areas of infestation but either the number of parasites was exceedingly small or large numbers were released out of synchronization with *R. buoliana* (Berry, 1939). Even the small number of parasites that were released at the proper time might have resulted in greater success had not the degree of infestation rapidly declined for other reasons soon after the releases were made³. Thus it appears that the early North America releases were highly unfavourable to proper establishment or to population build-up of even the most promising species, and that if releases were made under more favourable conditions many of the European parasites of *R. buoliana* might establish themselves here.

The current *R. buoliana* problem in Ontario and the neighbouring parts of the United States is aggravated by the planting of large areas to pure, even-aged stands of red or Scots pine. *R. buoliana* often gained access to the plantation in infested nursery stock and was provided with a concentrated and constant supply of food until the plantation closed some 15 to 25 years later. Under these conditions very heavy infestations of *R. buoliana* have developed in Connecticut (Friend, 1935) and Ontario (Watson and Arthur, 1959).

Although there are many parasites which attack *R. buoliana* and may hold it at low population levels in Europe, where mixed, uneven-aged forests predominate, it is doubtful if they could do so in the pure pine plantations of North America. Balch (1960) reached a similar conclusion in connection with the spruce budworm, *Choristoneura fumiferana* (Clem.), which is attacked by a long list of natural enemies. While some of these enemies do play an important role in maintaining low populations between outbreaks, they are unable to respond to rapid increases of the budworm brought about by favourable weather in an

³P. B. Dowden. Northeastern Forest Experiment Station, New Haven, Conn., U.S.A., in personal communication.

extremely favourable forest type. Thus the most we can expect is that *R. buoliana* parasites might become established in North America in areas where the host population is high and be able to maintain low host population levels after it has been reduced by an extremely cold winter or after the plantation has begun to close.

The heavy infestations of *R. buoliana* in large, pure pine plantations are difficult to control with parasites for still another reason. The present authors agree with Mesnil (1958) that a complex of oligophagous parasites can overtake and control an insect pest more quickly than one or more specific parasites. However, to be effective the parasites must have other hosts in close proximity to the *R. buoliana* infestation when the latter is low. All the external larval parasites of *R. buoliana*, both European and indigenous, as well as *A. nudibasis*, *P. turionellae*, and *I. conquisitor*, require alternate hosts which are scarce in the large pure pine plantations of North America. When present, parasites increase in abundance on *R. buoliana* only to become scarce in the next generation because of a lack of alternate hosts. Thus a large portion of the European parasite complex and all but one indigenous species, *Hyssopus thymus* Gir., is handicapped by North American silvicultural practices.

The present authors make the following recommendations regarding the biological control of *R. buoliana* in North America:

(1) *O. obscurator* and *T. turionum* are the most likely species to become established and give some measure of economic control.

(2) Where *O. obscurator* has proven to be ineffective, *T. interruptor* might be introduced into areas having mild winter temperatures. However, it is not generally recommended because it competes directly with the more valuable *O. obscurator*.

(3) The usefulness of *E. ruficollis* and *E. roborator* should be further investigated.

(4) Most species of parasites should be released in colonies of at least 300 mated females which are ready to oviposit. Releases should be made in large plantations or in one of many small plantations that are in the same area.

(5) Releases of the external larval parasites should be made in areas known to contain an adequate supply of alternate hosts.

(6) Releases should be made in infested pine plantations where Umbelliferae grow or have been planted to provide the adult parasites with an abundant supply of their favourite food.

(7) If a parasitic species is available from two or more areas, it should be collected where climatic conditions, especially low winter temperatures, are similar to those of the intended release area.

Summary

Surveys of the North American parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), showed few promising species. Four species were common: three external larval parasites and one pupal parasite. From the collections of infested shoots from six European countries, sixteen common parasites were obtained: seven internal larval, seven external larval, and two pupal parasites.

A detailed account is given of the releases and research done with each species with comments on the reasons for their apparent inefficiency.

Two species are considered valuable in the control of *R. buoliana*: the internal larval parasite *Orgilus obscurator* (Nees) and the pupal parasite *Tetrastichus turionum* (Htg.).

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An Old World Field Cricket Species in America (Orthoptera : Gryllidae : *Scapsipedus*)¹

By L. J. JOBIN² AND R. S. BIGELOW³

In April, 1959, field crickets were collected in Jamaica and brought alive to this laboratory for study. The great majority of these specimens were *Gryllus assimilis* Fabricius⁴, and it was assumed for some months that all the specimens collected belonged to this species. The senior author, however, noticed certain specimens that appeared to be distinctive; these were segregated and reared separately, crossing experiments were carried out between them and *Gryllus assimilis*, and the nymphal stages of both forms were compared. These studies revealed that two distinct species had been collected in Jamaica, and the unknown species was subsequently determined by Professor L. Chopard as *Scapsipedus marginatus* Afzelius and Brannius.

The genus *Scapsipedus* is widely distributed in Asia and Africa but, judging from available records, it is rare in the New World. *Scapsipedus limbatus* Saussure (a synonym of *S. marginatus* Saussure) has been recorded from Cuba and Jamaica by Rehn and Hebard (1915) and by Rehn (1917).

Specimens of this species in the Museum of Comparative Zoology at Harvard University are from Haiti as well as from Cuba and Jamaica. *Scapsipedus marginatus* has been established in the West Indies, therefore, for at least 45 years. An apparently introduced species, determined as *Scapsipedus micado* Saussure, was discovered recently at Huntsville, Alabama, by Dr. R. D. Alexander (Univ. of Michigan, pers. communication), and an undetermined species that probably belongs in this genus was collected in North Carolina in April, 1958 by R. S. Bigelow. The presence of this Old World genus in America poses interesting questions bearing on zoogeography, but further information on the distribution and differentiation of American *Scapsipedus* species is required before such questions can be answered. The aim of this paper is to facilitate recognition of *Scapsipedus marginatus* adults and nymphs by supplementing and enlarging on the original description.

The genus *Scapsipedus* was first described by Saussure (1877, *Melanges Orth.* Fasc. V : p. 407), chiefly from specimens of *Scapsipedus marginatus* (Afzelius and Brannius). Saussure distinguished the genus from other gryllines on head characteristics that are described by Chopard (1934) as follows:

"Avec les *Scapsipedus*, nous arrivons au groupe des *Gryllinae* chez lesquels la tête subit une déformation particulière due à un aplatissement très marqué de la face; cette déformation est toujours beaucoup plus accentuée chez les mâles que chez les femelles. C'est ainsi que, chez les *Scapsipedus*, qui représentent le

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⁴It is now clear that American field crickets previously referred to the genus *Acheta* cannot be treated as congeneric with the house cricket, *Acheta domesticus* L. and at the same time generically distinct from *Gryllus campestris* L. of Europe (the type species of the genus *Gryllus*). Cousin (1954, 1956, 1958) pointed out that, in terms of genitalic morphology and interfertility, these American species form a genetically closely related complex with *G. campestris* and *G. bimaculatus* of Europe which does not include *Acheta domesticus*. For similar reasons, Chopard (1955) suggested that American field crickets of this group should be transferred from *Acheta* to *Gryllus*. Alexander (1957) pointed out that even Dr. Gurney, who placed these American species in the genus *Acheta* (Gurney, 1950, 1951), suspected the arrangement might be rather artificial. Bigelow (1960) obtained hybrids from crosses between Jamaican *assimilis* and two North American species (*rubens* and *pennsylvanicus*), thus linking nearctic and neotropical species in a chain of interspecific fertility which is continued, through Cousin's work, to European *Gryllus* species. Recently, Mr. R. L. Randell of Macdonald College has completed a study of the male genitalia, chromosome number, and interfertility of the species concerned and has shown conclusively that these American field crickets belong in the genus *Gryllus* with *G. campestris* and not in *Acheta* with *A. domesticus*. Mr. Randell's paper will be published in the near future.

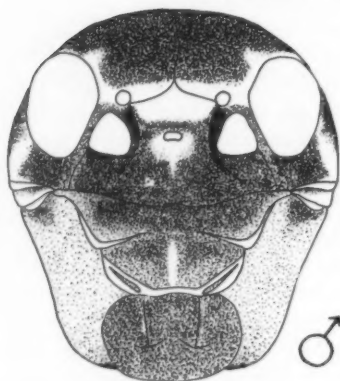
Scapsipedus marginatus

Fig. 1

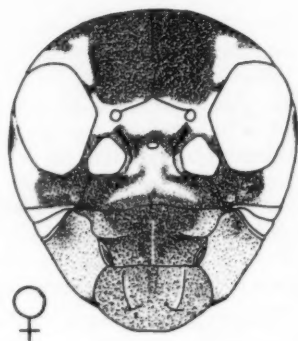


Fig. 2

Figs. 1-2. 1. *Scapsipedus marginatus*, male, anterior aspect of face. 2. *Scapsipedus marginatus*, female, anterior aspect of face.

type le moins spécialisé dans le groupe, les mâles sont reconnaissable à leur face un peu aplatie, tandis que les femelles sont absolument semblables à celles des *Gryllus*. Il en résulte que ces dernières, isolées, sont très difficiles à déterminer, d'autant plus que la variabilité est très grande dans le genre, tout comme chez les véritables *Gryllus*. Enfin, chez certaines espèces, le miroir élytral des mâles a tendance à se perdre la réticulation apicale."

As Chopard points out, the marked flattening of the face in the males which is the most distinctive feature of certain *Scapsipedus* species, is not marked in the type species, *S. marginatus*. The latter, however, can be distinguished readily from all other gryllines known to us by the distinctive yellow band on the face, and by the bicoloured abdomen. These characters are still easily discernible in specimens that have been on pins for over 45 years in the Harvard Museum of Comparative Zoology.

Scapsipedus marginatus was first described, by Afzelius and Brannius (1804), as follows:

"*Acheta marginata*, fusco-nigrescens, antennis corpore parum longioribus, hemelytris basi margine laterali lineaque longitudinali obsoleta albidis. Fig. 1, et 5.a.

Solem marem vidimus, qui statura magnitudine et etiam colore, quamvis multo saturatiore, *A. domesticæ* admodum est similis. Et fieri queat, ut ejus femina sit Fabricii *A. assimilis*, cujus vero differentia specifica adeo est mala, quamadmodum supra indicavimus, et descriptio adeo manca, ut sine exemplaris inspectione hac in re nihil certi adserere possimus. Interea, noster qualis est, dicamus.

Corpus septem et quod excurrit lineas longum paulloque plus quam duas latum, nigrescens subobscure. Caput atrum nitidum; Frons: maculis majusculis, media lanceolata inferius aucta, ut major et ovalis appareat, lateralibus junctis fascia lata helva, ad oculos et pone eos ad basin palporum exteriorum

Gryllus assimilis



Fig. 3

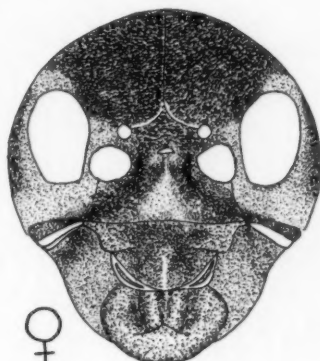


Fig. 4

Figs. 3-4. 3. *Gryllus assimilis*, male, anterior aspect of face. 4. *Gryllus assimilis*, female, anterior aspect of face.

producta pallidiore; *Oculi* olivaceo-hepatici; *Antennae* corpore aliquanto longiores fusco murinae: articulo primo subter lateribusque atro, super cum fossula sordide lutescente; *Processus* frontis arciformis nigricans, margine inferiore albidus. *Clypeus* piceus: gibbere obtuse carinato; *Palpi* straminei: articulis. A. bimaculatae et Mauri, praeter quam quod exteriorum quartus tertio sit paullo brevior; *Mandibulae* badiae apice atrae: dentibus 4 majoribus intermixtis 3 minoribus; *Maxillae* isabellinae apice badiae: denticulis duobus superioribus maximis nigris, inferiore minore lutescente, infimo setaceo pallidiore; *Galeae* subpilosae xerampelinae apice atrae.

Thorax latitudine aequali, subtilissime hirtus sordideque ater, versus latera isabellino obsolete variegatus, angulis laterum anticis macula pallidiore. *Hemelytra* ad anum vix porrecta; parum declivia, totâ basi margine utrimque laterali lineâque inter dorsum et latera obsoletâ sordide albida, plagâ dorsi elatâ lateribusque oblique lineatis praesertim antice atra ceterum glauco-fusca: nervis dilutioribus; *Alae* abdomine plus quam duplo longiores: cauda recta longitudine hemelytrorum. *Abdomen* nigrum cinereo sericeum: carina quadrata, pilis rufescentibus, ano glauco: *Seta* cauda alarum parum breviores declinatae. *Pedes* cum pectore laminisque cinerascemellei: pilis nigris commixtis atris et fuscis, *antici* quatuor: femoribus tibiis tarsisque ut in A. bimaculata et Mauro, *postici* duo desunt."

The same species was later redescribed by Chopard (1934) as follows:

"Un des Grillons les plus répandus en Afrique; de la taille d'un grand Grillon domestique, se reconnaît assez facilement à sa tête brune ornée d'une bande jaune à l'extrémité du rostre; les élytres sont, en général, un peu foncés sur le disque avec la bande humérale jaunâtre; il existe 4 ou 5 veines obliques chez le mâle. Le *Scapsipedus limbatus* Sauss. paraît en être une grande variété à 5-7 obliques chez le mâle. Quand au *Sc. Felderi* Sauss. il ne peut même pas être conservé comme variété car Saussure, ne donne aucun caractère permettant de le séparer

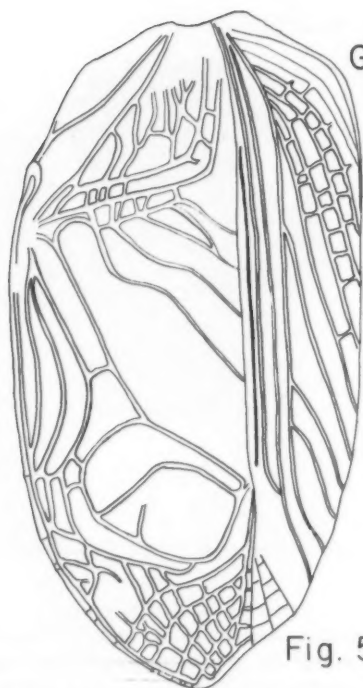


Fig. 5

G. assimilis

S. marginatus

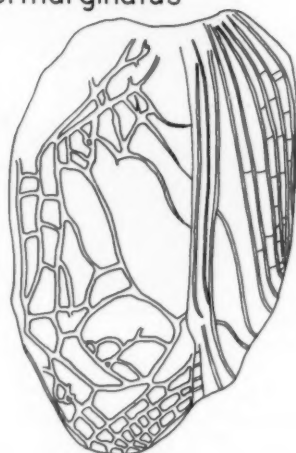


Fig. 6

Figs. 5-6. 5. *Gryllus assimilis*, male, dorsal aspect of right tegmen. 6. *Scapsipedus marginatus*, male, dorsal aspect of right tegmen.

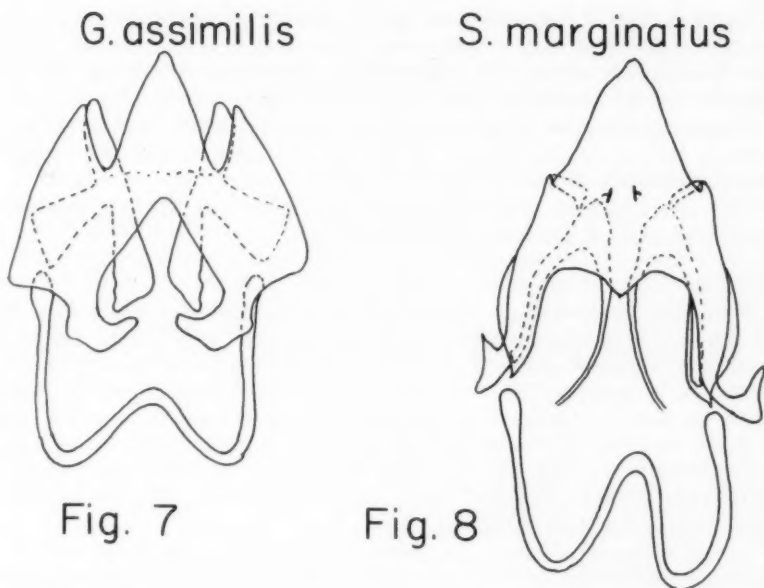
du *Sc. marginatus*, la forme de la tête étant variable suivant la grosseur des individus et ne pouvant fournir un bon caractère spécifique."

Redescription

The following descriptions are based mainly on first generation descendants of specimens collected in Jamaica, near Mandéville, and subsequently reared in the laboratory. No differences were detected between these laboratory-reared specimens and field-collected specimens from Jamaica, Haiti, or Cuba.

Adult Male.

A wide, transverse yellow band extending the full width of the face between the compound eyes just above the antennal sockets, and containing the lateral ocelli; yellow bands of approximately equal width extending from the posterior edge of the compound eye to the posterior articulation of the mandible on either side (viewed anteriorly with the naked eye, all three bands appear to form a single yellow arch extending upward from the posterior mandibular articulations and crossing the face above the antennal sockets, but interrupted by the compound eye on either side); pleurostoma yellow between the anterior and posterior articulations of the mandible, forming a distinct "V" with the yellow band extending antero-dorsally from the posterior mandibular articulation to the compound eye; median ocellus light yellow, forming a distinct spot on the dark brown background of the face, usually with a small area of yellow pigment extending downward from its ventral edge; usually with a yellow band of



Figs. 7-8. 7. *Gryllus assimilis*, dorsal aspect of male epiphallus. 8. *Scapsipedus marginatus*, dorsal aspect of male epiphallus.

variable width extending from the dorsal edge of the compound eye caudad across the occiput to the posterior rim of the head (this band is often indistinct and sometimes absent); sometimes with a variable number of indistinct longitudinal yellow bands on the occiput; remainder of head dark brown, nearly black in some specimens. These yellow facial markings are, to our knowledge, peculiar to *S. marginatus*. (*A. domesticus* L. has a very broad transverse yellow band on the occiput behind the compound eyes which is absent in *S. marginatus*); postclypeus dark brown, lighter on lateroventral edges, preclypeus brown, grading into testaceous along ventral edge; labrum dark brown; palpi grey. Mandibles orange and very large relative to those of the female or to those of most other gryllines of either sex (see Figs. 1-4).

Pronotum approximately 1.5 times as wide as long, slightly convex on the posterior margin; disc dark brown to black, marbled with brown or yellow at the posterolateral corners; lateral lobes dark brown to black with a yellow spot at the antero-ventral angle.

Abdomen dark brown to black dorsally, with a row of testaceous spots on either side of the mid-dorsal line (usually concealed beneath the elytrae and wings); pleuron light yellow, sharply demarcated from the dark tergites; sternum yellow to light brown with a longitudinal row of grey spots along each lateral edge and two narrow longitudinal grey lines, one on either side of the mid-ventral line.

Fore and mid femora grey, mottled with brown; hind femora reddish-brown, heavily striated on the external and upper internal faces; tibiae very dark brown, posterior tibiae with seven or eight spines on the external, seven on the internal margins; spines reddish-brown with dark tips.

Tegmina shorter than abdomen; mirror squarish, divided behind the middle by curved and oblique veins (shorter than those of *G. assimilis*, as shown in Figs. 5 and 6); a distinct testaceous longitudinal stripe along the lateral angle and continuing around the anterior edge of each tegmen.

Hindwings either very long (extending well beyond the caudal tip of the abdomen) or very short (concealed beneath the tegmina and not extending beyond the third or fourth abdominal tergum).

The male genitalia differ distinctly from those of *Gryllus assimilis* in numerous features, as shown in Figs. 7 and 8.

Adult female.

Yellow markings on head usually more extensive than in males; entire surface of head posterior to compound eyes usually yellow apart from a dark brown spot behind the compound eye on each side; yellow below the median ocellus and between the antennal sockets with two yellow ventral arms extending laterally beneath the antennal socket on either side (in some females this median yellow spot is confined to a small area beneath the median ocellus, as in males); genae and pleurostomata usually yellow except for a narrow brown band along the ventral edge of each compound eye; longitudinal yellow lines on the occiput usually more distinct than in males.

Lateral edges of pronotal disc lighter than in males; entire ventral half of lateral lobe light yellow on either side, with a distinct dark band along the dorsal half just below the light lateral edge of the disc. Forelegs lighter grey than in male; tegmina usually shorter than in male, often failing to extend caudad beyond the fourth abdominal tergite.

Nymphs.

Head very dark brown with a narrow, yellow inverted "Y" along the ecdysial sutures in fifth instar and younger nymphs or with a broad yellow band between and including the lateral ocelli in sixth to eleventh instar nymphs; posterior half of occiput light brown (but not yellow or testaceous as in *Acheta domesticus*); usually with yellow markings posterior to the compound eyes and with parallel longitudinal yellow lines on the occiput.

Terga of thorax and abdomen with dark brown spots on a pale testaceous ground colour dorsally, and with a white longitudinal ecdysial line along the entire length of the body from the head to the caudal end of the abdomen; dark grey, parallel lines of variable thickness on either side of the white mid-dorsal line on the abdominal terga; ventro-lateral edges of thoracic and first two abdominal terga very dark brown, forming a distinct dark band along each side from the prothorax to the third abdominal segment; pleural and sternal regions of the abdomen very pale, distinctly lighter than terga.

S. marginatus nymphs are most likely to be confused with those of *Gryllus assimilis* Fabricius or with *Acheta domesticus* L.

G. assimilis nymphs are readily distinguishable from those of either *S. marginatus* or *A. domesticus* by their reddish-brown or grey pleurostomal and sternal areas. In both *S. marginatus* and *A. domesticus* the corresponding areas are pale yellow or very light grey, and are sharply demarcated from the darker abdominal terga along a distinct longitudinal line on each side of the abdomen.

In *A. domesticus* nymphs the head is predominantly yellow or pale testaceous with three dark brown transverse bands: one (very broad) between the inner dorsal angles of the compound eyes, another (narrower) between the antennal

sockets, and a third along with ventral edge of the labrum. In both *S. marginatus* and *G. assimilis* the head is predominantly dark brown with only a narrow yellow inverted "Y" along the line of the ecdysial suture (i.e. coronal and frontal sutures) in all *G. assimilis* and in *S. marginatus* nymphs below the sixth instar, or with only a single yellow transverse band in sixth to eleventh instar *S. marginatus* nymphs.

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Book Review

A Review of the Soldier Flies or Stratiomyidae of California, by Maurice T. James, Bull. of the Calif. Insect Survey, Vol. 6, No. 5, pp. 79-122, plates 6-10 (54 figs.), 19 maps. University of California Press, Apr. 22, 1960. Price \$1.00.

This is another in the series of straightforward, bulletin-type publications on the systematics of the insects of California. Primarily, it provides keys for the identification of the subfamilies, genera, subgenera and species of the Stratiomyidae (Diptera) that are known, or are expected, to occur in California. In addition, it provides some interesting notes and observations on the biological and phylogenetic relationships of the family to other groups of flies and points out some evolutionary trends within the family.

The author's purpose is to present a comprehensive survey of all the Stratiomyidae (except the Pachygastrinae and the *Euparyphus-Aochletus* complex, now under study by Dr. Kenneth J. Kraft and Dr. John A. Quist) of the Pacific Coast, and to provide entomologists with a means for identifying Californian material of this family. It is the first study of this kind for this region.

Mr. James is well qualified to fulfill this purpose, having studied the family intensively on a world basis for nearly thirty years and having produced more than 100 scientific papers dealing mostly, but by no means entirely, with the taxonomy of soldier flies. Thus, the "Soldier Flies or Stratiomyidae of California" is based on a solid foundation of long experience in, and a broad knowledge of, the group. It exhibits the same thoroughness and practicality as does his well known bulletin on "The Flies that Cause Myiasis in Man".

The collecting data represent the accumulation of more than a quarter of a century and include material drawn from a dozen or more institutions holding collections of Californian insects. The first key is to the subfamilies and genera of California Stratiomyidae; it is followed by separate keys to the species and subspecies treated under each genus. All keys (opposing couplet type) are clearly and concisely composed and are well documented with references to explanatory figures.

For each genus descriptive information is given on the numbers of species included, its geographic distribution, and the habits of the larvae and adults. Similarly, each species is treated as to its synonymy, broad geographical range, occurrence in California and its relationships to other species, seasonal distribution, habits, etc. An index and a résumé of the species, genera and subfamilies treated would be useful. For the record, the paper deals with 14 genera (in seven subfamilies) containing 69 species. A few of these, not definitely known from California, are included in the keys but are not dealt with in further detail.

Nineteen maps show the detailed distributions in California and general distributions in the United States of almost all of the species treated in the text. There are three plates of figures, mostly dealing with abdominal patterns, head profiles, and wing venation. Although they are somewhat diagrammatic they are accurate and clear and serve their purposes admirably.

This work is a "must" for specialists, teachers and students who wish to study the soldier flies of the Pacific coast region, and, since many of the species treated are not confined to California, it will be very useful to everyone who studies these flies. It is a regional treatment of the group and, as the author states, "generalities have often been sacrificed to utility, and the keys will fail to work for some of the extralimital species of genera included". However, it faithfully fulfills its primary purpose, and being the only work of its kind for California and adjoining states, it is a real addition to the knowledge of Stratiomyidae.

J. F. McALPINE

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